Chapter 16
Auxin and Tropisms

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Abstract From the very beginnings, attempts to identify mechanisms underlying polar auxin transport in higher plants have been intimately linked to studies on the regulation of plant tropisms. Already in the nineteenth century Charles Darwin came up with a concept, suggesting that a transmissible signal might be involved in controlling directional plant growth in response to an environmental stimulus. Much later, plant physiologists identified auxin as a candidate molecule that could mediate tropic growth responses. However, it was not until establishment of *Arabidopsis* genetics and novel molecular techniques at the end of the twentieth century that enabled the characterization of auxin-signaling pathways and resulted in mechanistic insights into control of polar auxin transport and its significance for plant tropisms. In this chapter, essential aspects of the current framework of molecular events are presented, highlighting the role of auxin in directional plant growth.

1 A Moving Story

When taking basic courses in plant physiology at the—then brand new—first Biozentrum building in Vienna, Professor Karl Burian entertained us with a conversation he had with one of the construction site engineers. They walked through one of the greenhouses, and by accident the engineer touched one of the mimosas that were cultivated for student courses. The plant responded to this stimulus, and after a few seconds of silence, the stunned engineer exclaimed: "For a moment I thought that it's alive!"

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E. Zažímalová et al. (eds.), *Auxin and Its Role in Plant Development*,
DOI 10.1007/978-3-7091-1526-8_16,

The experienced professor used this anecdote as a starter for his lecture on plant movements, one of the most fascinating aspects of plant physiology. When going through the old notes on this lecture, it seems that not much has changed in conceptual terms: Plants sense an environmental stimulus that triggers transmission of endogenous signals, ultimately resulting in, sometimes quite fast responses like the nastic movements of mimosa leaves, or, comparably slow growth responses like organ movement in accordance with the gravity vector or gravitropism. Some of these concepts are ancient, dating back long before Darwin's influential book on the movement of plants (Darwin and Darwin 1881). However, what has changed in recent years is the availability of powerful molecular techniques, producing amazing insights into principles of signal perception and transduction that guide plant movements.

2 Plant Movements: Overlapping and Distinct Concepts

Plants are continuously exposed to variations in their respective environment, which are perceived by a sophisticated sensorium of receptors and signaling pathways in order to adjust growth parameters accordingly. Given that higher plants are sessile, they have evolved mechanisms that allow them to modify their organ growth in response to environmental stimuli. These activities differ from preprogrammed autonomous plant movements, as they depend on perception of an external stimulus. Two major types of such responses, tropism and nastic movements have been described, where tropic responses depends on the direction of the stimulus, like a chemical gradient or local variations in illumination, whereas nastic movements summarize nondirectional responses. A large variety of different stimuli cause tropic responses in plants, and a range of different tropisms have been described. Moreover, they come in different flavors. Depending on the direction of movements, either toward or away from the external stimulus, resulting movements are referred to as positive or negative tropisms. In special cases, even transversal tropisms have been observed, like, for instance, strawberry runners, defined by a growth direction on the soil's surface, i.e., perpendicular to the main growth axis.

Empirical records describing *phototropism* (or *heliotropism*), i.e., directional movement of plant organs in response to a light stimulus, date back to Greek philosophers. For the longest time though, Aristotelian views, that discriminated plants from animals based on their supposed "insensitivity," hampered proper interpretation of this growth response (for an excellent summary on the history of phototropism research, see Whippo and Hangarter 2006). It was not until the seventeenth century, that researchers began to hypothesize that tropic curvature involves an actual growth response and it took until the late nineteenth century, to show that phototropism is an inductive response, triggered by a directional light stimulus (Sharrock 1672; Darwin and Darwin 1881; Sachs 1882). Darwin's interpretation of growth experiments suggesting that organ circumnutation functions as a uniform mechanism that drives directional plant growth responses could not be

verified in subsequent experiments (Darwin and Darwin 1881). However, he was the first to come up with a concept, predicting that a transmissible signal would control events, leading from perception of a stimulus to the actual growth response. This concept still holds true and represents one of the cornerstones of contemporary models for plant tropisms.

The term *geotropism* (nowadays most often replaced by the term *gravitropism*) was introduced by Albert B. Frank (1868) and by Julius von Sachs (1868) and defines directional growth movements of plants in response to gravity. Early experiments by Andrew Knight and Henry Johnson (1829) proposed that downward growth of roots might be controlled by gravity. But it was the work especially by Sachs, who introduced the clinostat and initiated a systematic analysis of plant organ bending in response to external stimuli, that led to our current views on mechanisms of plant tropisms (Sachs 1879, 1892).

Thigmotropism involves perception of and response to mechanical stimulation (Migliaccio et al. 2009), whereas *chemotropism* describes directional movement of plant organs in response to chemical gradients. A prominent example is pollen tube chemotropism that describes directed pollen tube growth from the stigma to ovules in a process that seemingly involves pollen tube attraction by chemotropic factors (Chae and Lord 2011). *Hydrotropism* finally could be considered a special case of chemotropism, in which directional growth of roots is influenced by the availability of water, a vital growth response that has been described already by early plant physiologists like Sachs (1872).

3 Plant Movements and the Influence of Auxin: A Historical Perspective

Plant tropisms depend on spatiotemporal control of asymmetric organ growth. This typically involves differential cell expansion in distinct portions of an organ, like in the apical region of hypocotyls bending toward light. In some instances, differential cell elongation appears to be intimately linked to the control of cell proliferation, as in graviresponding root tips. Regardless of mechanisms involved, it appears that activity of the phytohormone auxin is crucial for all tropisms, and there is now convincing evidence that this growth regulator represents Darwin's transmissible signal.

A number of plant researchers deserve credit for initial characterization of the hormone and for putting forward working models that explain the contribution of auxin to the control of organ bending, thereby generating a solid foundation for our current understanding of polar auxin transport (PAT). Based on Darwin's experiments, which show that removal of the very tip of canary grass coleoptiles will block organ bending toward a light source (Darwin and Darwin 1881), researchers tested the concept of a transmissible signal causing this growth response. It was Peter Boysen Jensen (1910), who demonstrated the existence of such a

transmissible signal that will penetrate through a layer of gelatine, introduced subapically into oat coleoptiles. Furthermore, by inserting impermeable mica sheets into cuts made into coleoptiles before phototropic stimulation, Boysen Jensen was able to conclude that signal transmission at the shaded side of illuminated coleoptiles is essential for their bending, an elegant, first demonstration of signal gradient formation taking place in plants (Boysen Jensen 1913). Discovery and initial characterization of auxin, as a mediator of tropic growth responses, came from work by Frits Went (1926) and Nikolai Cholodny (1927), whereas the chemical characterization of the compound was achieved by Kögl and Haagen-Smits (1931). Went and Cholodny, independently, suggested quite similar mechanisms by which auxin could influence organ bending, now known as the Cholodny–Went theory (Went and Thimann 1937). In simple terms, this theory proposes that lateral, unequal auxin distribution within organs, induces differential growth, ultimately causing organ curvature (Cholodny 1928; Went 1928; Fig. 16.1a).

Whereas the Cholodny–Went theory offers a simple explanation for organ bending, it is not fully resolved, if lateral auxin transport to the shaded side of organs is the only cause for phototropic curvature. Additional mechanisms, such as light-induced growth inhibition at the illuminated side of the organ (Overbeek 1932; Baskin 1986), or variable photo-inactivation of auxin (Kögl and Schuringa 1944), could contribute to the growth response as well (Fig. 16.1a). In addition, spatiotemporal variations in cellular auxin sensitivity could lead to differential auxin responsiveness and resulting growth adjustments (Kang and Burg 1974; Fig. 16.1a). Experimental evidence in support of the Cholodny–Went theory was provided by Winslow Briggs and coworkers, demonstrating light-controlled lateral auxin redistribution in phototropically responding corn coleoptiles (Briggs et al. 1957). Some years later, Briggs showed a direct correlation between phototropic coleoptile curvature and auxin found on the shaded side of the organ, suggesting that it is the steepness of lateral auxin concentration gradients that defines phototropic organ bending (Briggs 1963). Related studies demonstrated that unilateral illumination by blue light is sufficient for establishment of a lateral auxin gradient in coleoptiles, thus predicting the involvement of blue-light responsive photoreceptors in gradient establishment (Pickard and Thimann 1964; Gardner et al. 1974).

Alternatives to upregulation of lateral auxin transport in response to unilateral illumination have been proposed. For example, work by Shen-Miller and colleagues (1969) suggested light-controlled asymmetric inhibition of PAT in phototropically stimulated oat coleoptiles. Recent, molecular characterization of auxin transport activities in Arabidopsis hypocotyls undergoing phototropic curvature provided evidence for both scenarios; induction and downregulation of PAT (Christie et al. 2011; Ding et al. 2011), pointing toward a more complex array of events involved in light-mediated control of auxin distribution.

Similar to the situation in above-ground organs, control of root tropisms appears to involve establishment of a lateral auxin gradient. That is, an environmental stimulus like gravity would promote auxin accumulation at the “lower” side of a horizontally positioned root, where it would cause growth inhibition, resulting in a

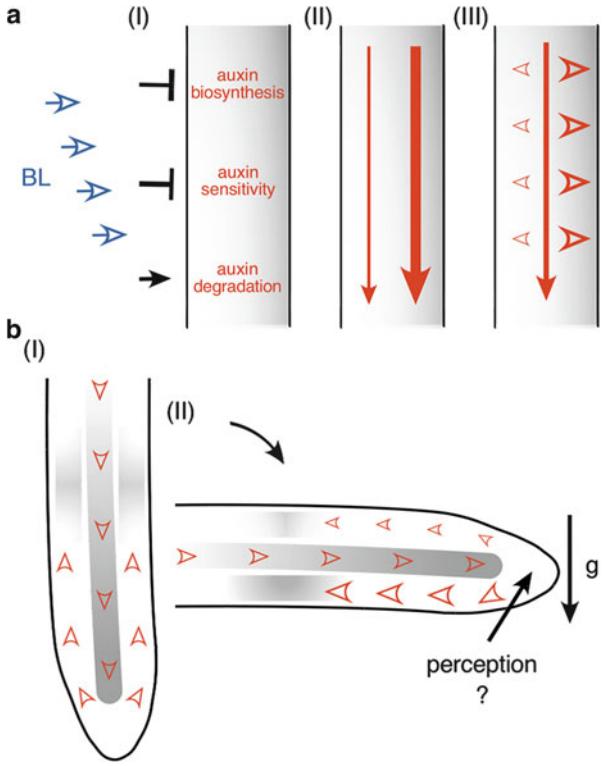

Fig. 16.1 Suggested modes of auxin action upon tropic organ growth. (**a**) Differential auxin responses upon phototropic stimulation by unilateral illumination with blue light (BL) were suggested to result from local variations in auxin biosynthesis, sensitivity, or degradation (I). In alternative models, asymmetric auxin flow from the apical portion of the stimulated organ (*red arrows*) was suggested to induce differential organ growth (II). This might result from local inhibition or induction of PAT. Another model suggested establishment of a lateral auxin concentration gradient, via differential lateral auxin transport (*red arrowheads*), with more auxin transferred into the shaded, elongating portion of the organ (III). (**b**) Fountain model describing auxin transport routes in root meristems. Rootward auxin transport in the stele mediates auxin accumulation in the root tip (*red arrowheads*). From there it is redistributed for further shootward transport via outer cell layers into the root meristem elongation zone (I). Upon gravistimulation (*black arrow* indicates direction of gravity vector), more auxin is transported to the lower side of the root tip, resulting in asymmetric, shootward auxin flow into the elongation zone (*red arrowheads*), ultimately causing organ bending (II). *Shaded areas* indicate zones accumulating auxin and/or exhibiting increased auxin responsiveness

downward bending of the root tip (Kaufman et al. 1988). Differences in cell expansion rates in gravistimulated roots have been described, specifically in the Distal Elongation Zone (DEZ) a region proximal to the mitotically active zone in root meristems (Ishikawa et al. 1991). In numerous studies, a complex interplay of spatiotemporal variations in cell elongation has been described, and variations have been observed when comparing responses under different conditions or in different

species (Pilet and Ney 1981; Nelson and Evans 1986; Firn and Myers 1989; Ishikawa et al. 1991; Ishikawa and Evans 1997). In Arabidopsis for example, gravistimulation was shown to induce transient, differential elongation in the DEZ, reflected in growth inhibition at the lower side, whereas growth at the upper side appears stimulated, contributing to the control of root bending (Mullen et al. 1998). This likely reflects distinct and overlapping growth responses, ensuring proper interpretation of gravity signals during the continuous growth of roots.

Linking differential root elongation in bending roots to auxin has been difficult, mainly due to technical limitations in the determination of variations in auxin concentrations in tissue as fragile as root tips. Moreover, in those cases in which researchers managed to determine auxin distribution in graviresponding roots, differences in auxin concentration were rather small, which made it difficult to link root gravity responses to lateral auxin concentration gradients in the DEZ (Mertens and Weiler 1983; Young et al. 1990). Perception and transduction of the gravity signal requires the root cap, verified by numerous experiments demonstrating that root decapitation blocks any further tropic growth responses (Darwin and Darwin 1881; Juniper et al. 1966). This indicates involvement of a signal that, after gravity perception in the root cap, would get transmitted into the root bending zone. In a modified version of the Cholodny–Went hypothesis it was proposed that auxin itself would function as that signal, first being translocated via the stele into the columella root cap, from where it would get redistributed into the root elongation zone, with asymmetries in auxin flow, resulting in directional root growth (Konings 1968; Hasenstein and Evans 1986; Boonsirichai et al. 2002). This fountain model for PAT in root meristems accounts for variations in auxin flow rates and consequences for directional root growth and is meanwhile supported by several studies, describing molecular determinants of PAT (Fig. 16.1b).

4 Molecular Determinants of Auxin Transport and Signaling in the Regulation of Tropisms

It was not until the advent of *Arabidopsis thaliana* as a model system for plant molecular genetics that led to identification of molecular determinants of signaling cascades involved in plant tropisms. In this section, selected aspects of stimulus perception as well as transmission and translation of auxin signals into tropic growth responses are summarized.

4.1 Phototropism

Stimulus Perception

In the nineteenth century Julius von Sachs demonstrated that blue light is most efficient for induction of phototropic responses (Sachs 1882), but it took another century and mutant screens performed in Arabidopsis to characterize the genes involved. In such screens, hypocotyl phototropism mutants that no longer bend toward a light source were identified (Khurana and Poff 1989; Liscum and Briggs 1995), which eventually led to characterization of *NON PHOTOTROPIC RESPONSE1* (*NPH1*) an AGC-type kinase protein (Huala et al. 1997; Galvan-Ampudia and Offringa 2007). This protein, together with its close relative *NPH1-LIKE 1* (*NPL1*; Jarillo et al. 2001), represents key regulators of blue light-mediated tropic responses and hence were renamed *phototropin1* (*phot1*) and *phototropin2* (*phot2*; Briggs et al. 2001). Both proteins are characterized by two Flavin Mononucleotide (FMN)-binding sites, so-called LOV (light-, oxygen- or voltage-sensing) domains that bind FMN chromophores noncovalently in the dark. Blue light causes covalent binding of FMN to the LOV domains, which results in conformational changes that expose the C-terminal phototropin kinase domain (Salomon et al. 2000; Christie et al. 2002). Blue light-induced kinase activation then appears to cause phototropin autophosphorylation at conserved Serine residues, a modification indispensable for phototropic responses (Christie et al. 1998, 2002; Sakai et al. 2001; Inoue et al. 2008). Although phototropins seem to represent the only class of receptors capable of sensing directionality of a blue light stimulus (Sakai et al. 2001), additional light receptors have been implicated in the regulation of tropic growth responses, acting via, e.g., modulation of transcriptional control and intracellular protein distribution (Lariguet and Fankhauser 2004; Han et al. 2008; Wu et al. 2010; Kami et al. 2012). This apparent involvement of additional light receptors might reflect parts of a complex network of interactions among distinct classes of light receptors, essential for fine-tuning of tropic growth responses (Hohm et al. 2013).

Identification of phototropin-interacting proteins elucidated potential links to auxin transport. Cloning of *NPH3*, which was originally identified as another hypocotyl phototropism mutant, revealed a protein featuring conserved domains that function in protein–protein interaction (Motchoulski and Liscum 1999): A coiled-coil domain, in the C-terminal portion of NPH3 is required for its interaction with phot1 (Motchoulski and Liscum 1999), whereas a BTB/POZ (broad-complex, tramtrack, bric à brac/Pox virus and zinc finger) domain mediates interaction with ROOT PHOTOTROPISM2 (RPT2), a protein similar to NPH3 and belonging to the NRL (NPH3/RPT2-Like) protein family (Inada et al. 2004; Sakai 2005). NPH3 has been found to localize to specific domains at the plasma membrane, similar to its interaction partner phot1 (Motchoulski and Liscum 1999). In addition its rice ortholog has been implicated in auxin redistribution in phototropically responding

coleoptiles (Haga et al. 2005); however, functions of NPH3 and related proteins in mechanistic terms remained elusive.

Work by Roberts and others (2011) might provide answers to questions regarding the function of NRL proteins. The authors found that NPH3 acts as adaptor protein that binds to CUL3, an SCF-type E3 ubiquitin ligase complex subunit, apparently facilitating phot1 ubiquitylation in a light-dependent manner (Roberts et al. 2011). Under conditions of low blue light intensity, phot1 is mono(multi) ubiquitylated, whereas higher irradiation intensities correlated with phot1 polyubiquitylation. Such different ubiquitylation modes could have a strong impact on the fate of phot1, with monoubiquitylation affecting intracellular sorting, and polyubiquitylation triggering proteasome-dependent phot1 degradation (Roberts et al. 2011). Resulting variations in phot1 distribution and/or abundance were suggested to feed back on PAT in Arabidopsis hypocotyls (Roberts et al. 2011).

Additional members of the NRL family have been linked to the regulation of directional growth responses. Next to *RPT2,* required for root phototropism and demonstrated to interact with phot1 (Sakai et al. 2000), *NAKED PINS IN YUCCA/ENHANCER OF PINOID/MACHI-BOU* (*NPY/ENP/MAB*) genes were recently shown to function in auxin-controlled processes involving root gravitropism (Treml et al. 2005; Cheng et al. 2007, 2008; Furutani et al. 2007, 2011; Li et al. 2011). By analogy to interaction of NPH3 and phot1, there is evidence for similar crosstalk between NPYs and additional AGC-kinases involving PINOID (PID) and some of its close homologs (Cheng et al. 2007, 2008). Given the function of PID in adjusting directionality of PAT by controlling phosphorylation status and localization of PIN-FORMED (PIN) auxin transport proteins (Friml et al. 2004; Michniewicz et al. 2007), it is tempting to speculate about a function for NPY proteins, similar to the one shown for NPH3. In such a scenario, NPYs might function as adaptors, recruiting E3 ubiquitin ligases for ubiquitylation of PID or related AGC kinases, in order to modulate phosphorylation and intracellular sorting of auxin transport proteins (Michniewicz et al. 2007). Indirect evidence supporting such a scenario comes from a recent study, demonstrating mislocalization of PINs auxin transport proteins in *npy* mutant background, presumably causing pronounced aberrations in PAT (Furutani et al. 2011). Moreover, a function in the regulation of PIN sorting was recently suggested for NPH3, which together with phot1 appears to modulate PIN2 localization in root meristem cells (Wan et al. 2012). We still need to await further experimental proof for such a concept, but a regulatory module consisting of SCF-ubiquitin E3 ligases, NRL adaptor proteins, and AGC-type protein kinases could represent a highly versatile regulatory hub, integrating environmental and intrinsic cues and their various impacts on PAT.

Transmission of the Light Stimulus

After perception of a tropic stimulus, it is necessary to adjust auxin signaling and responses in respective tissues, in order to orchestrate growth events. Transmission

of the initial light signal to the auxin transport/signaling machinery has remained a black box for quite some years, until recently, two reports provided mechanistic insights (Christie et al. 2011; Ding et al. 2011). Christie and others demonstrate interaction between phot1 and auxin efflux carrier ABCB19 (ATP-BINDING CASSETTE B19), which appears to result in ABCB19 phosphorylation and inhibition of its transport activities (Christie et al. 2011). The authors suggested that such inhibition of auxin transport, preferentially in the illuminated portions of hypocotyls, could establish an ABCB19 activity gradient, with more hormone being transported at the shaded side from the hypocotyl apex into the bending zone (Christie et al. 2011). In this model, an auxin concentration gradient would be established already in the hypocotyl apex (Fig. 16.2a, b). In another model suggested by Ding and coworkers establishment of lateral auxin gradients takes place directly in the bending zone of hypocotyls (Ding et al. 2011). Together with additional plasma membrane-localized PIN-type auxin transport proteins, PIN3 has been proposed to act in hypocotyl phototropism (Friml et al. 2002; Haga et al. 2005), which is expressed at the plasma membrane of hypocotyl stele and endodermis cells. The authors found that unilateral blue-light treatment resulted in a relocation of endodermal PIN3 reporter signals, giving rise to polar distribution at the plasma membrane that would favor lateral auxin transport from the illuminated towards the shaded side of hypocotyls (Ding et al. 2011; Fig. 16.2c and 16.3a). Such control of PIN3 distribution apparently depends on intracellular protein sorting via ADP ribosylation factor guanine nucleotide exchange factor (ARF-GEF) GNOM-pathways and is controlled by PID. According to this model, blue-light-mediated gradual downregulation of *PID* transcription enforces PIN3 polarization due to resulting variations in PID kinase activities (Ding et al. 2011; Fig. 16.2d).

Both mechanisms offer plausible scenarios, connecting blue-light signaling and auxin gradient establishment in the control of hypocotyl phototropism. It remains to be resolved, however, how these distinct mechanisms converge to control lateral auxin gradient establishment (Haga and Sakai 2012; Sakai and Haga 2012; Hohm et al. 2013).

Regardless of mechanisms ultimately causing auxin gradient establishment in illuminated hypocotyls, variations in auxin concentration need to be perceived by hormone receptors and translated further into local adjustments of gene expression programs that drive differential growth. Some lines of evidence suggest involvement of $SCF^{TIR1/AFB}$-type E3 ubiquitin ligases that function as auxin receptors and are essential for transcriptional responses induced by the growth regulator (see Chap. 6 and Dharmasiri et al. 2005). Möller and others (2010) demonstrated phototropism defects in *tir1 afb1 afb2 afb3*, deficient in four F-box proteins, each of which constituting a subunit of SCF auxin receptor complexes. Additional evidence for involvement of the SCF-auxin receptor pathway comes from analysis of *MASSUGU2(MSG2)/IAA19* one of the likely substrates for $SCF^{TIR1/AFB}$ complex-mediated polyubiquitylation (Tatematsu et al. 2004). *MSG2* represents one out of 29 Aux/IAA proteins in Arabidopsis (Liscum and Reed 2002), several of which have been demonstrated to be short lived and degraded in response to auxin by means of $SCF^{TIR1/AFB}$ E3 ubiquitin ligase activity (Gray et al. 2001). Analysis of

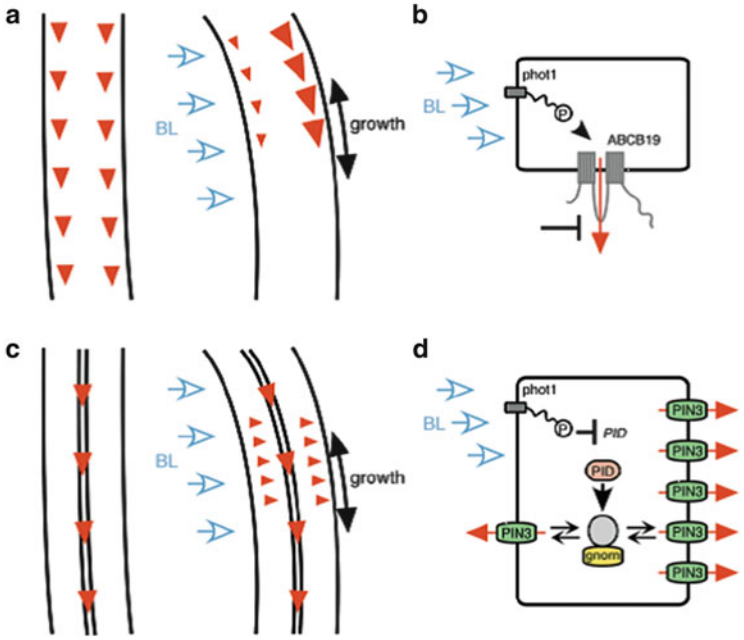

Fig. 16.2 Current models describing establishment of lateral auxin gradients upon phototropic stimulation of Arabidopsis hypocotyls. (**a**) According to Christie and colleagues (Christie et al. 2011), differential auxin flow is established in the most apical portion of unilaterally illuminated hypocotyls (*blue arrows*), with more auxin transported at the shaded side to induce asymmetric growth in the hypocotyl bending zone. (**b**) This response is proposed to involve phot1-mediated phosphorylation of ABCB19 resulting in local inhibition of ABCB19-mediated rootward auxin transport (*red arrow*). (**c**) Ding and colleagues (2011) proposed PIN3-mediated lateral auxin transport in the hypocotyl bending zone toward the shaded side (*small red arrowheads*). (**d**) Mechanistically, this response is suggested to involve phot1-controlled inhibition of *PID* transcription, resulting in local adjustments in PIN3 distribution at the plasma membrane controlled by PID- and GNOM-dependent sorting pathways

dominant, presumably stabilized, *msg2* alleles revealed severe defects in hypocotyl tropisms and alterations in auxin-controlled gene expression, suggesting involvement of *MSG2* in the control of differential hypocotyl growth responses (Tatematsu et al. 2004). Aux/IAA proteins form heterodimers with AUXIN RESPONSE FACTOR (ARF) transcriptional regulators, and these dimers are suggested to attenuate *ARF* function in transcriptional control (Guilfoyle and Hagen 2007). Intriguingly, Yeast-2-Hybrid assays demonstrated interaction between *MSG2* and *NPH4*/*ARF7* (Tatematsu et al. 2004), representing an *ARF* gene with a nonredundant function in hypocotyl phototropism (Harper et al. 2000). This led to models in which variations in $SCF^{TIR1/AFB}$-mediated MSG2 turnover cause adjustments in *NPH4*/*ARF7*-controlled transcriptional programs, essential for phototropic organ bending (Tatematsu et al. 2004).

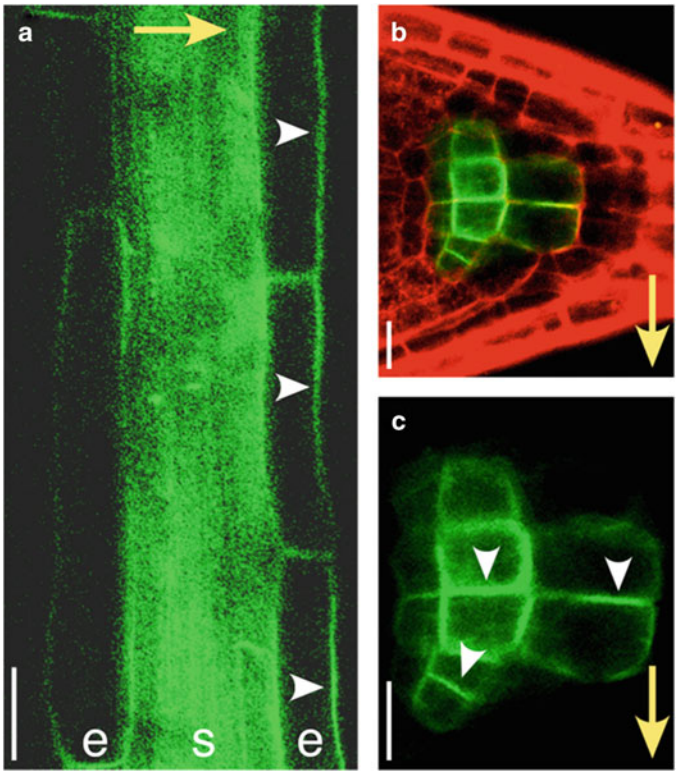

Fig. 16.3 Relocation of PIN auxin carriers as potential determinants of directionality of auxin transport in *Arabidopsis thaliana*. (**a**) Distribution of PIN3:YFP signals (*green*) in unilaterally illuminated *PIN3::PIN3:YFP* hypocotyl cells (*yellow arrow*). *White arrowheads* indicate enrichment of fluorescent signals at the lateral, outer plasma membrane domain of endodermis cells at the shaded side. This might result in increased, lateral auxin flow. (**b**, **c**) Accumulation of PIN3:YFP signals (*green*) at the *bottom side* of columella root cap cells gravistimulated for 10 min (*yellow arrow* indicates direction of gravity vector). *White arrowheads* in (**c**) indicate signal accumulation at the *lower side* of these cells. *Red signals*: Propidium iodide cell wall staining. Scale bars: $a = 50$ µm; b, $c = 10$ µm

Only little is known about downstream targets of the *MSG2*/*NPH4* regulatory module that could bring about physiological adjustments essential for differential cell elongation. A function in differential growth has been attributed to expansins, a group of proteins implicated in controlled cell wall loosening, particularly under conditions of acidic pH, thereby allowing for turgor-driven cell expansion (Rayle and Cleland 1970; Hager et al. 1971; Cosgrove 2005). Whilst it is not fully resolved, how expansins function in mechanistic terms, expression of some members of this gene family has been associated with hypocotyl elongation (Caderas et al. 2000). Furthermore, by analyzing unilaterally illuminated *B. oleracea* seedlings, Esmon and colleagues demonstrated differential expression of presumptive *NPH4*/*ARF7* target genes, including expansins *EXPA1* and *EXPA8* in hypocotyls,

with more transcripts accumulating at the elongating, shaded side (Esmon et al. 2006).

Apart from a role of $SCF^{TIR1/AFB}$ in phototropism, auxin signaling via AUXIN BINDING PROTEIN1 (ABP1) could be involved as well. Evidence for auxin binding by ABP1 was first provided in maize coleoptile membrane preparations (Hertel et al. 1972; Batt and Venis 1976). Subsequently, molecular cloning and functional characterization suggested auxin perception by ABP1 at the periphery of the plasma membrane (Barbier-Brygoo et al. 1989; Inohara et al. 1989; Tillmann et al. 1989). Clearcut molecular evidence for ABP1-controlled signaling at the plasma membrane was provided recently, demonstrating that ABP1 functions as positive regulator of clathrin-mediated endocytosis (Robert et al. 2010). Upon auxin binding, ABP1 effects on endocytic sorting of plasma membrane proteins are attenuated (Paciorek et al. 2005; Robert et al. 2010). This might affect the equilibrium between intracellular and plasma membrane localized pools of auxin carrier proteins, which in turn might impact on PAT activities essential for phototropic bending. Consistent with this model, defects in phototropism have been described for *abp1*/*ABP1* heterozygote seedlings (Effendi et al. 2011).

In addition to a function in modulating auxin flow, ABP1 appears relevant for apoplastic acidification and control of cell expansion (Cosgrove 2005). Auxin binding by ABP1 correlates with plasma membrane hyperpolarization, resulting from elevated plasma membrane-(PM)-H^+ATPase activity that is detectable already within minutes (Barbier-Brygoo et al. 1989; Rück et al. 1993). This has been attributed to auxin-induced PM-H^+ATPase phosphorylation as well as to increased abundance at the plasma membrane (Hager et al. 1991; Takahashi et al. 2012). Together with comparably slow $SCF^{TIR1/AFB}$-mediated transcriptional responses, such rapid ABP1-induced proton extrusion might constitute a regulatory module for transmission of auxin signals, controlling phototropic growth.

Root Phototropism

Compared to the wealth of information, addressing regulation of phototropism in above-ground organs, substantially less is known about the situation in roots. The more so, as root phototropism appears to be a less uniform response than light-regulated growth of aerial organs (Kutschera and Briggs 2012) and as the ecological significance of soil-borne organs responding to light remains unclear (Kiss et al. 2003; Galen et al. 2007). Roots of several plant species, including those of *Arabidopsis* exhibit negative phototropism (Wiesner 1884; Kutschera and Briggs 2012), which allowed the characterization of mutants with deficiencies in light-controlled directional root growth (Okada and Shimura 1992; Liscum and Briggs 1995). Some of these mutant alleles turned out to be allelic to *phot1*, suggesting participation of the blue light receptor in modulating light-responsive root growth. Notably, *phot1* appears to be expressed in the root meristem (Sakamoto and Briggs 2002), and analysis of PHOT1-GFP reporter expression in roots demonstrated a positive correlation between root growth efficiency and phot1 abundance in cells

close to the soil surface, suggesting that light perception by root-expressed phot1 is involved in directional root growth (Galen et al. 2007).

In a study by Wan and colleagues (2012), the authors provide indirect evidence for asymmetric distribution of auxin in unilaterally illuminated roots, with more auxin accumulating at the shaded side. Control of such asymmetric auxin distribution might involve *PIN2* activity, indicated by reduced responsiveness of a *pin2* null allele, exposed to blue light. Notably, blue light appears to modulate intracellular distribution of a PIN2 reporter protein by mechanisms that seemingly require NPH3 (Wan et al. 2012). It remains to be determined, as to how such regulation of PIN2 localization might affect PAT in phototropically responding roots.

4.2 Gravitropism

Gravity Perception and Signaling

Quite similar to analysis of phototropism, early experiments addressing root gravitropism identified sites of gravity perception as well as zones that respond with differential growth to the stimulus (reviewed in, e.g., Boonsirichai et al. 2002; Arnaud et al. 2010). However, unlike phototropism, a gravity receptor, acting analogous to light receptors has not been identified.

Physical ablation experiments in which the root cap, the very tip of the root, was removed demonstrated its significance for gravity responsiveness (Darwin and Darwin 1881; Juniper et al. 1966). In more recent years, manipulation of Arabidopsis root meristems by genetic or laser-mediated removal of the root cap confirmed earlier findings and characterized starch-accumulating columella root cap cells as potential gravity sensors (Blancaflor et al. 1998; Tsugeki and Fedoroff 1999). These and numerous further studies are in agreement with the starch-statolith hypothesis, originally coined by Gottlieb Haberlandt, suggesting that sedimentation of starch-filled amyloplasts (statoliths) within specialized statocytes is essential for perception of variations in the direction of the gravity vector (Haberlandt 1900). Analogous to statolith sedimentation in roots, relocation of plastids in endodermal cells was suggested to function in gravity perception in above-ground organs (Kiss et al. 1997; Morita 2010).

A role for starch-accumulating plastids in gravity perception is supported by analysis of starch metabolism mutants, like *pgm1* alleles, deficient in *PHOSPHOGLUCOMUTASE1*, which exhibit a reduced, but still significant gravity responsiveness (Caspar and Pickard 1989; Sack 1991). This led to modified concepts, suggesting that starch is important but not absolutely required for initial gravity perception by plastids in gravity responsive cells (Morita 2010). However, to this day, mechanisms that would translate gravity-induced plastid relocation into a cellular response remain elusive, both, in roots and stems. Mutual interactions between the actin cytoskeleton and plastids have been implicated in early events of gravity signal perception (Hou et al. 2003; Nakamura et al. 2011), which might

affect activity of mechano-sensitive ion channels (Sievers et al. 1989; Perbal and Driss-Ecole 2003). This in turn might cause variations in secondary messenger signaling and/or in a shift in cytoplasmic pH, but the physiological significance of these responses is not fully resolved (Daye et al. 1984; Sievers et al. 1984; Gehring et al. 1990; Fasano et al. 2001; Plieth and Trewavas 2002; Boonsirichai et al. 2003; Perera et al. 2006). Intriguingly, some of these responses, like Ca^{2+} and inositol trisphosphate signaling have been linked to control of auxin transport, which might reflect a function in controlling auxin distribution in gravistimulated organs (Lee et al. 1984; Ettlinger and Lehle 1988; Hasenstein and Evans 1988; Zhang et al. 2011; Cho et al. 2012).

The Role of Auxin Transport

A combination of genetics, cell biology, and biochemistry identified the molecular machinery orchestrating PAT in higher plants (see Chaps. 5 and 8) and established its function in control of tropisms. Identification of auxin response mutants provided genetic evidence, as these mutants exhibit often quite pronounced defects in directional growth responses (Lincoln et al. 1990; Pickett et al. 1990; Timpte et al. 1995). Mutations in the AUXIN TRANSPORTER PROTEIN1 (AUX1) permease-like protein result in pronounced resistance to externally applied IAA and cause strong defects in tropisms, which led to the suggestion that AUX1 functions in cellular uptake of auxin thereby modulating directional growth (Pickett et al. 1990; Bennett et al. 1996; Stone et al. 2008). Indeed, functional analysis in heterologous systems demonstrated auxin transport activity, capable of translocating IAA across membrane boundaries (Yang et al. 2006). Characterization of additional mutants deficient in root gravitropism led to identification of proteins required for cellular auxin efflux. Mutants deficient in *AGRAVITROPIC ROOT*/*ETHYLENE INSENSITIVE ROOT1*/*PIN-FORMED2*/*WAVY GROWTH6* (*AGR*/*EIR1*/*PIN2*/*WAV6*) turned out to be defective in a plasma membrane protein expressed in the outer cell layers of root meristems and became the founding member of the plant-specific family of PIN-type auxin efflux carrier proteins (Chen et al. 1998; Luschnig et al. 1998; Müller et al. 1998; Utsuno et al. 1998). Furthermore, mutations affecting members of the p-glycoprotein PGP/ABCB family exhibit alterations in auxin distribution and in control of tropisms, arguing for an involvement of plant ABC-transporters in directional growth responses (Noh et al. 2001; Terasaka et al. 2005; Nagashima et al. 2008). For both, plasma membrane-localized PINs and ABCBs, there is now experimental evidence for their activity as auxin carrier proteins (Petrášek et al. 2006; Yang and Murphy 2009), but it took extensive analysis of auxin carrier expression, subcellular localization, and its dynamics to obtain a comprehensive picture of events, orchestrating auxin distribution in graviresponding organs.

According to the fountain model, acropetal/rootward PAT in the stele would deliver auxin from the shoot into the root tip. PIN1 auxin efflux carrier expressed in the stele appears to be involved in this process, indicated by defects in rootward

PAT in *pin1* loss-of-function alleles, and by PIN1 localization at the lower, basal end of stele cells, which would favor transport toward the root tip (Okada et al. 1991; Gälweiler et al. 1998; Geldner et al. 2001). Redistribution of auxin for further basipetal/shootward transport toward the elongation zone is suggested to take place in the root cap (Hasenstein and Evans 1988), and might involve activity of PIN3 and PIN7 efflux carriers that localize to the plasma membrane of root cap columella cells (Friml et al. 2002; Kleine-Vehn et al. 2010). Upon gravistimulation, both PINs rapidly accumulate at the plasma membrane domain at the lower side of columella cells (Friml et al. 2002; Kleine-Vehn et al. 2010; Fig. 16.3b, c). As a result, auxin would be relocated predominantly to the lower side of the root tip ready for its passage to the DEZ, where it would induce differential cell elongation and root bending (Ottenschlager et al. 2003; Band et al. 2012). Such a PIN-dependent redistribution mechanism is also utilized in lateral roots, allowing defined auxin flux and lateral root gravitropic set point regulation (Rosquete et al. 2013). PIN relocation in columella cells is detectable within a few minutes after gravistimulation and presumably occurs via ARF-GEF GNOM-dependent protein transcytosis (Friml et al. 2002; Kleine-Vehn et al. 2010; Fig. 16.4a, b). In addition, mutants affected in *ALTERED RESPONSE TO GRAVITY1*/*ROOT AND HYPOCOTYL GRAVITROPISM* (*ARG1*/*RHG*) or *ARG1-LIKE2* (*ARL2*) were shown to exhibit defects in gravistimulated relocation of PIN3 (Harrison and Masson 2008). ARG1 and ARL2 represent DnaJ-domain containing peripheral membrane proteins, implicated in regulation of vesicular transport that might link early events in gravity perception to the control of directional auxin transport (Boonsirichai et al. 2003; Harrison and Masson 2008; Fig. 16.4a, b).

Somewhat surprisingly, *pin3* or *pin7* single mutants and its combinations exhibit only subtle defects in root gravitropism, suggesting redundant activities of additional auxin transport proteins (Kleine-Vehn et al. 2010). This differs from mutants deficient in AUX1 and PIN2, which exhibit pronounced agravitropic root growth and defects in PAT, indicating rate-limiting activities in the control of root gravitropism (Bennett et al. 1996; Chen et al. 1998; Luschnig et al. 1998; Utsuno et al. 1998; Rashotte et al. 2000). Indepth analysis of AUX1 function revealed a significant role for AUX1 expression in lateral root cap cells proximal to the central root cap, as conditional *aux1* mutants lacking *AUX1* expression in these cells fail to exhibit gravitropic root growth (Swarup et al. 2005). Further auxin transport via lateral root cap and epidermis cells into the DEZ requires PIN2 (Müller et al. 1998; Blilou et al. 2005; Vieten et al. 2005), with a tight regulation of its localization and turnover. PIN2 protein stability regulation is seemingly essential for establishment of a lateral auxin gradient in graviresponding roots (Paciorek et al. 2005; Abas et al. 2006; Fig. 16.4c, d). Specifically, analysis of PIN2 signals in gravity-responding roots revealed establishment of a transient expression gradient, with more PIN2 accumulating at the lower side vs. the upper side of horizontally positioned roots (Paciorek et al. 2005; Abas et al. 2006). This involves antagonistic processes, with PIN2 retention at the plasma membrane of epidermis cells at the lower side, and enhanced PIN2 endocytosis and vacuolar targeting at the upper side, altogether resulting in differential auxin flow toward the DEZ, and -ultimately-

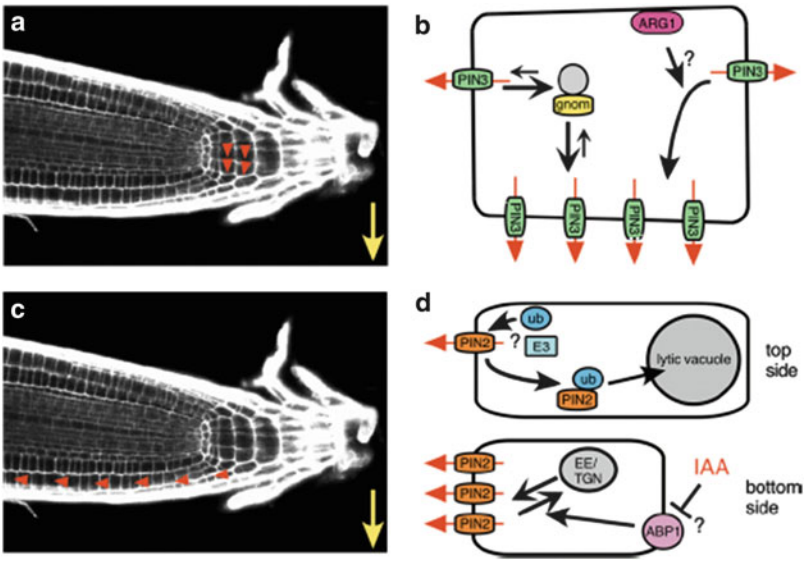

Fig. 16.4 Mechanisms potentially involved in auxin relocation to the lower portion of gravistimulated Arabidopsis root meristems. (**a**) Auxin relocation to the lower side of the root tip is suggested to initiate within minutes after gravistimulation (*yellow arrow* indicates direction of the gravity vector; *red arrowheads* highlight directionality of auxin flow). (**b**) Rapid relocation of PIN3 auxin carrier to the plasma membrane domain at the lower side of gravistimulated root cap cells involves GNOM ARF-GEF regulated sorting and transcytosis. In addition, a function for peripheral membrane protein ARG1 in PIN3 relocation has been shown but remains to be characterized in mechanistic terms. (**c**) At later stages, auxin flow is increased at the lower side of root meristems, when compared to the upper side (*red arrowheads*), eventually causing downward bending of the root tip. (**d**) Control of differential PIN2 expression has been implicated as an essential determinant for this process. At the upper side vacuolar PIN2 targeting is suggested to cause a reduction in plasma membrane-localized PIN2 levels. Vacuolar PIN2 targeting has been suggested to require its (poly)-ubiquitylation, however, E3 ubiquitin ligase controlling this step is still unknown. At the lower side, PIN2 appears to be stabilized at the plasma membrane promoting auxin transport into the root elongation zone. This response is suggested to involve inhibition of ABP1-mediated clathrin-dependent PIN2 endocytosis into Early Endosome/Trans Golgi Network (EE/TGN) compartments. Inhibition of ABP1 activity might arise as a consequence of its binding to auxin. Whether such ABP1–auxin interaction occurs at the cell's periphery, or intracellularly, is not known

downward bending of the root tip (Paciorek et al. 2005; Abas et al. 2006; Kleine-Vehn et al. 2008; Robert et al. 2010; Leitner et al. 2012). It is not fully resolved, how such differential protein sorting might be regulated, but apparently PIN2 ubiquitylation signals variations in its sorting and proteolytic turnover in an auxin-dependent feedback regulatory loop (Sieberer et al. 2000; Leitner et al. 2012; Baster et al. 2013). This regulatory switch allows for continuous adjustments in auxin flow rates in the coordination of directional root growth (Band et al. 2012), but molecular determinants, sensing, and controlling the

interplay between auxin levels and PIN2 sorting remain to be determined in more detail (Fig. 16.4d).

PIN expression gradient formation could as well be involved in control of hypocotyl gravitropism. Rakusova and others observed asymmetric abundance of PIN3-GFP reporter signals in endodermis cells of gravistimulated hypocotyls that would favor auxin flow to the organ's lower, elongating side (Rakusova et al. 2011). Such gravity-induced PIN3 relocation in hypocotyls was found to require GNOM ARF-GEF and PID activity, which appears comparable to PIN3 relocation upon phototropic stimulation and further highlights the critical role of intracellular protein sorting in the control of tropic growth responses (Ding et al. 2011; Rakusova et al. 2011).

Variations in auxin distribution, resulting from differential auxin transport activities in graviresponding organs, appear to cause induction of distinct transcriptional programs that would induce differential cell expansion. By analogy to the transcriptional output resulting from phototropic signaling, transcriptional responses to gravistimulation could involve activity of Aux/IAA and ARF proteins, as indicated by agravitropic growth phenotypes associated with corresponding mutant and misexpression lines (Okushima et al. 2005; Wang et al. 2005; Weijers et al. 2005; Yan et al. 2013). However, detailed insights into phenotypic consequences of variable transcriptional control of downstream target loci are still limited. Perhaps, transcriptome analyses based on cell-sorting approaches will help to elucidate differences in gene expression at a sufficiently high resolution, both, over time, and in different portions of graviresponding organs (Birnbaum et al. 2005).

4.3 Hydrotropism

Molecular analysis of physiological events controlling directional plant growth in response to humidity gradients has been problematic for the longest time, due to difficulties in separating gravitropic and hydrotropic responses (Sachs 1872). Notably, decapitation and ablation experiments revealed a role for the columella root cap in moisture gradient perception (Jaffe et al. 1985; Miyazawa et al. 2008), thus, overlapping with sites of gravity perception and raising questions as to how root tip cells perceive and transmit these different environmental stimuli (Takahashi et al. 2009). However, in the 1980s, an agravitropic pea mutant was found to exhibit positive hydrotropism, suggesting that control of these tropic responses requires distinct regulatory switches (Jaffe et al. 1985). There is only limited information available on early events of hydrotropic signaling, which was suggested to involve Ca^{2+} signaling and was found to coincide with degradation of starch granules in columella root cap cells, the significance of which remains elusive (Takano et al. 1997; Takahashi et al. 2003).

Conflicting evidence suggests involvement of auxin in regulation of hydrotropism. Auxin transport inhibitors, like 2,3,5-triiodobenzoic acid (TIBA) were found

to block hydrotropism in some plant species, whereas in Arabidopsis no comparable effect was observed (Mizuno et al. 2002; Kaneyasu et al. 2007). Likewise, while some reports suggest local differences in auxin signaling and/or concentration in roots exposed to moisture gradients, other reports failed to verify such variations (Mizuno et al. 2002; Takahashi et al. 2009). Moreover, Arabidopsis loss-of-function mutants deficient in *PIN2* and *AUX1* exhibit normal root hydrotropism, which uncouples Arabidopsis hydrotropic responses from these key mediators of PAT in root meristems (Takahashi et al. 2002).

Mutant screens performed in Arabidopsis allowed for characterization of determinants involved in root hydrotropism (Eapen et al. 2003; Kobayashi et al. 2007). Cloning of *MIZU-KUSSEI1* (*MIZ1*) revealed a gene of unknown function that is strongly expressed in root columella cells; however, its function in root hydrotropism remains unanswered (Kobayashi et al. 2007). Notably, when analyzing lateral root formation in *MIZ1* loss-of-function and overexpression lines, it turned out that *MIZ1* acts as a negative regulator of lateral root formation in an auxin-dependent manner (Moriwaki et al. 2011). This could be linked to variations in free IAA content, with *miz1* roots accumulating more auxin than wild-type controls and might suggest that *MIZ1* function in root hydrotropism relates to modulation of auxin levels (Moriwaki et al. 2011).

Cloning of *MIZ2* provided additional indirect evidence for an involvement of auxin in regulation of hydrotropism. This mutant turned out to represent a novel allele of ARF-GEF *GNOM*; however unlike *gnom* alleles described earlier, $gnom^{miz2}$ does not exhibit comparable defects in overall plant morphology and in gravitropic growth responses (Geldner et al. 2004; Miyazawa et al. 2009). These findings indicated a role for GNOM-dependent vesicle sorting in the regulation of hydrotropism, and, given the function of GNOM in controlling localization of auxin transport components (Geldner et al. 2003), it is tempting to speculate about similar, potentially subtler defects in $gnom^{miz2}$. Limited or delayed GNOM-dependent rerouting of auxin carrier proteins might account for moderate variations in auxin distribution or signaling, causing growth defects restricted to hydrotropism. However, no variations in auxin carrier protein localization or abundance have so far been described for *miz2* (Moriwaki et al. 2013). Notably, MIZ1 dosage effects on lateral root formation are blocked by $gnom^{miz2}$, suggesting indirect effects of GNOM on MIZ1-mediated variations in auxin homeostasis (Moriwaki, et al. 2011). Mechanisms controlling such crosstalk remain to be determined.

5 Concluding Remarks

More than a century after pioneering experimental work by early plant physiologists, a decent framework of molecular events controlling directional plant growth responses, is finally available. Even though current models still suffer from major shortcomings, like the vaguely understood mechanism of gravity-perception, we experienced the evolution of a once uncertain idea of transmissible signals being

involved in tropism to sophisticated molecular models, underpinning various functions of auxin in these growth processes. With all these concepts available, attracting students probably would have been easier for our professor.

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