© 2015. Published by The Company of Biologists Ltd | Journal of Cell Science (2015) 128, 1–7 doi:10.1242/jcs.159418

CELL SCIENCE AT A GLANCE

Auxin transporters and binding proteins at a glance

Peter Grones[1,2] and Jiří Friml[1,2,3,*]

ABSTRACT

The plant hormone auxin is a key regulator of plant growth and development. Differences in auxin distribution within tissues are mediated by the polar auxin transport machinery, and cellular auxin responses occur depending on changes in cellular auxin levels. Multiple receptor systems at the cell surface and in the interior operate to sense and interpret fluctuations in auxin distribution that occur during plant development. Until now, three proteins or protein complexes that can bind auxin have been identified. SCF^{TIR1} [a SKP1–cullin-1–F-box complex that contains transport inhibitor response 1 (TIR1) as the F-box protein] and S-phase-kinase-associated protein 2 (SKP2) localize to the nucleus, whereas auxin-binding protein 1 (ABP1), predominantly associates with the endoplasmic reticulum and cell surface. In this Cell Science at a Glance article, we summarize recent discoveries in the field of auxin transport and signaling that have led to the identification of new components of these pathways, as well as their mutual interaction.

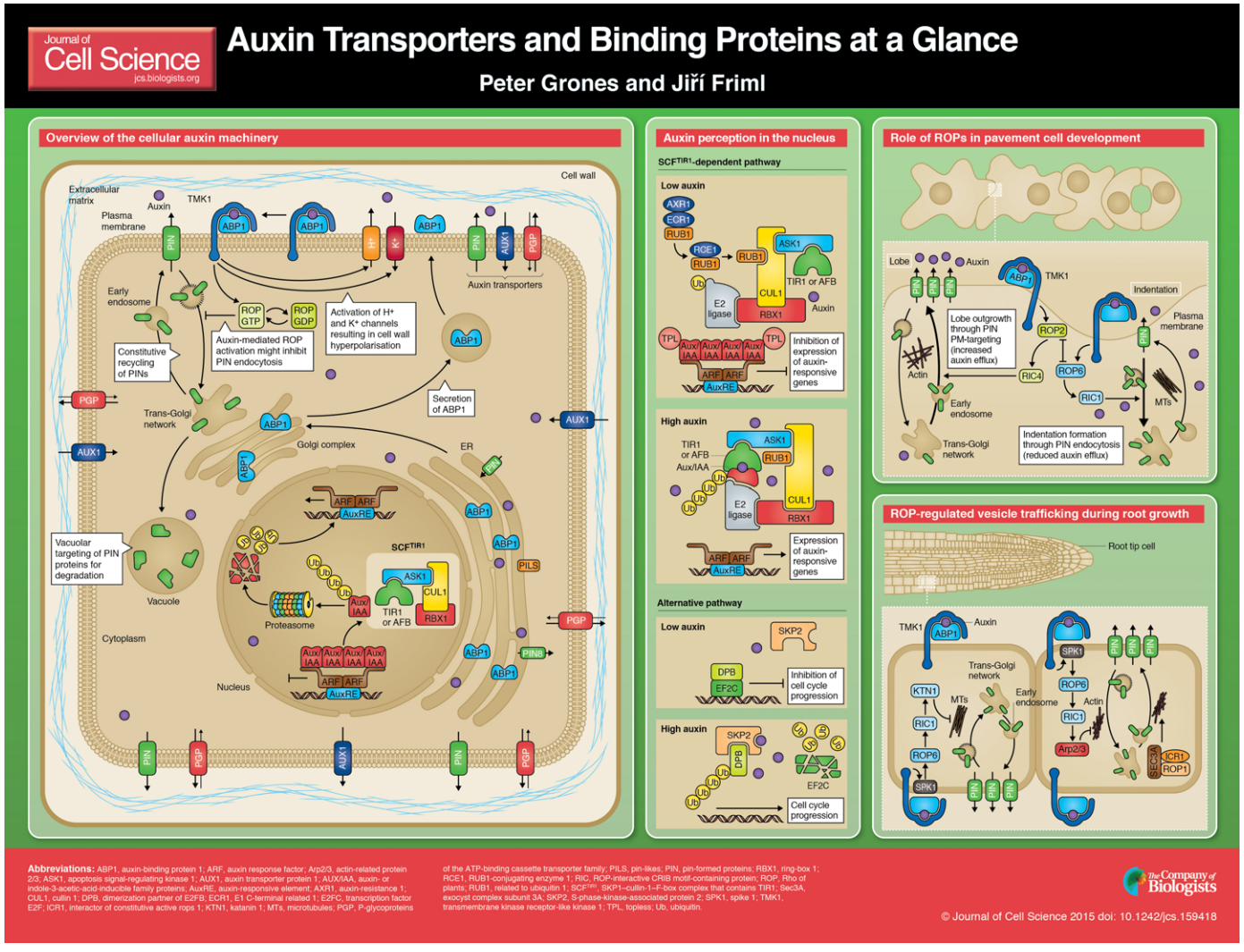
KEY WORDS: Auxin, Signaling, Transporters

[1]Institute of Science and Technology (IST) Austria, 3400 Klosterneuburg, Austria. [2]Department of Plant Systems Biology, Flanders Institute for Biotechnology (VIB) and Department of Plant Biotechnology and Bioinformatics, Ghent University, BE-9052 Gent, Belgium. [3]Mendel Centre for Plant Genomics and Proteomics, Masaryk University, CEITEC MU, CZ-625 00 Brno, Czech Republic.

*Author for correspondence (jiri.friml@ist.ac.at)

Introduction

The plant hormone auxin [chemically indole-3-acetic acid (IAA)], acts as a main coordinative signal in plants. It modulates plant growth and development by controlling



Journal of Cell Science

Journal of Cell Science (2015) 128, 1–7 doi:10.1242/jcs.159418

fundamental cellular processes, such as cell division, expansion and differentiation (Mockaitis and Estelle, 2008). Cellular auxin responses typically depend on auxin concentrations that mainly result from intercellular auxin transport and auxin biosynthesis, as well as metabolism. Over the past years, auxin transport proteins and their regulators have been characterized in detail, broadening our knowledge with regard to the polar auxin transport mechanism and, hence, the formation of the auxin gradient, organogenesis and differences in growth resulting in organ bending (Ganguly et al., 2012; Vanneste and Friml, 2009). Transport of auxin is usually accomplished by the combination of two pathways: a long-distance pathway, in which auxin is transported from its area of synthesis (i.e. from the shoot toward the root, through phloem tissues) (Ljung et al., 2005; Swarup et al., 2001); and a short-distance pathway that mediates cell-to-cell auxin transport through specific auxin influx and efflux carriers (Grunewald and Friml, 2010). There are four main classes of active auxin transporters in *Arabidopsis thaliana*: pin-formed proteins (PIN), proteins of the auxin transporter protein 1 (AUX1) and auxin transporter-like protein (LAX) family (hereafter AUX1/LAX), P-glycoproteins (PGP) of the ATP-binding cassette (ABC) transporter family, and pin-likes (PILS), which we will discuss below. Besides this, we will characterize three identified auxin receptor systems – those mediated by (1) SCF^{TIR} [a SKP1–cullin-1–F-box complex that contains transport inhibitor response 1 (TIR) as the F-box protein], (2) S-phase-kinase-associated protein 2 (SKP2), both of which are localized in the nucleus, and (3) ABP1, which localizes predominantly at the endoplasmic reticulum (ER) and the cell surface.

Auxin transporters

PIN proteins act as auxin exporters, and, with some exceptions, such as PIN5 or PIN8, they have a polar localization, being present at a particular plasma membrane region within the cell where they participate in directional auxin transport (Petrášek et al., 2006; Wisniewska et al., 2006). This process is required for the proper auxin distribution during various plant development processes, such as root meristem formation (Blilou et al., 2005; Friml et al., 2002), tropic responses (Abas et al., 2006; Baster et al., 2012; Ding et al., 2011; Rakusová et al., 2011), lateral organ development (Benková et al., 2003; Reinhardt et al., 2003) or embryo development (Friml et al., 2003; Weijers et al., 2005). PIN5 and PIN8 are localized at the ER where they presumably regulate auxin homeostasis by pumping auxin into and out of the ER lumen (Dal Bosco et al., 2012; Ding et al., 2012; Mravec et al., 2009).

The localization and maintenance of a polarized distribution of PIN proteins at the plasma membrane is a dynamic process that is required for cell polarity, differential auxin distribution and tissue patterning. PIN proteins are internalized constitutively through the clathrin-coated vesicle machinery (Dhonukshe et al., 2007; Kleine-Vehn and Friml, 2008) and are then recycled back to the plasma membrane (see poster). These processes are regulated by various ADP-ribosylation factor (Arf) GTPases, Arf guanine-nucleotide-exchange factors (Arf GEFs), such as GNOM (Kleine-Vehn et al., 2008), GNOM-like 1 (Richter et al., 2007; Teh and Moore, 2007) and BEN1/MIN7 (Tanaka et al., 2009), and Arf GTPase-activating proteins (Arf GAPs), such as VAN3, which partially acts in concert with GNOM (Naramoto et al., 2010). One of the important cellular regulators of the polar targeting of PIN proteins is phosphorylation, which is mediated by the serine/threonine protein kinase pinoid (PID), which leads to apical targeting of PIN proteins, and dephosphorylation by protein phosphatase 2A, which leads to basal PIN protein targeting (Michniewicz et al., 2007).

AUX1/LAX proteins are auxin influx carriers that are mostly responsible for auxin transport from the apoplast into the cytoplasm (Bennett et al., 1996; Swarup et al., 2001; Swarup et al., 2008). This family of four proteins regulates different developmental processes, such as lateral root formation (AUX1 and LAX3) or cotyledon vascular patterning (LAX2) (Swarup et al., 2008; Péret et al., 2012). Uniformly localized PGP proteins at the plasma membrane are involved in the ATP-dependent influx and efflux of auxin (Noh et al., 2001; Geisler and Murphy, 2006). In contrast to PINs, they are stably retained at the plasma membrane regardless of any internal or external signal and, hence, possibly mediate the basal intercellular transport of auxin (Geisler et al., 2003; Cho et al., 2012). Based on the structural similarity to the PINs, the PIN-likes (PILS) protein family has been identified; these proteins localize to the ER and also participate in auxin homeostasis at the ER (Barbez et al., 2012). Both the PIN and PILS protein families are specific to the clade of green plants, with PILS proteins being evolutionary older, because they are found already in unicellular algae (Feraru et al., 2012; Viaene et al., 2013).

Recently, the walls are thin 1 (WAT1) protein has been identified as a tonoplast-localized auxin transporter that is also involved in maintaining the intracellular auxin homeostasis (Ranocha et al., 2013). Thus, both intracellular and intercellular auxin transport systems together ensure the optimal cellular auxin concentration that is required for mediating plant growth and development.

Changes in cellular auxin concentration are transduced by auxin signaling systems to mediate different cellular responses. Three auxin receptor or co-receptor systems have been revealed and their contributions to auxin signaling have been clarified in the past few years, as discussed below.

Auxin perception by three receptor systems

The best-characterized auxin perception system is the co-receptor composed of transport inhibitor response 1 (TIR1) or auxin signaling F-box (AFB) proteins, and auxin- or indole-3-acetic-acid-inducible family proteins (hereafter AUX/IAA), which regulates auxin-dependent transcription in the nucleus (Ruegger et al., 1998; Dharmasiri et al., 2005a; Kepinski and Leyser, 2005; Tan et al., 2007; Calderón Villalobos et al., 2012). More recently, SKP2a has been found to be able to bind auxin and to be one of the crucial regulators of cell division (Jurado et al., 2010). Finally, ABP1 has been found to be a key player in fast non-transcriptional auxin responses (Rück et al., 1993; Steffens et al., 2001; Robert et al., 2010; Xu et al., 2010; Xu et al., 2014).

Auxin-mediated transcriptional regulation by TIR1

TIR1 was first identified in a forward-genetic screen for mutants that are resistant to auxin transport inhibitors (Ruegger et al., 1997). TIR1 and the AFB proteins are F-box components of a nuclear SCF-type E3 ubiquitin ligase (see below). In the presence of high auxin concentrations, the TIR1- or AFB-containing SCF complex targets the transcriptional AUX/IAA repressors (29 members in *Arabidopsis*) for degradation by the 26S proteasome by mediating their polyubiquitylation (see poster) (Gray et al., 2001; Dharmasiri et al., 2005b; Kepinski and Leyser, 2005; Petroski and Deshaies, 2005; Tan et al., 2007; dos Santos Maraschin et al., 2009). Degradation of AUX/IAAs leads to release of auxin-response factors (ARFs), which are transcription

Journal of Cell Science (2015) 128, 1–7 doi:10.1242/jcs.159418

factors, from the AUX/IAA–ARF heteromer, resulting in ARF–ARF dimerization and induction of expression of auxin target genes (Guilfoyle and Hagen, 2007; Korasick et al., 2014, Nanao et al., 2014). Auxin-dependent co-immunoprecipitation and yeast two-hybrid assays have revealed that TIR1 and ARFs have a different affinity toward various AUX/IAA family members, depending on the particular pair (Calderón Villalobos et al., 2012; Gray et al., 2001; Greenham et al., 2011; Shimizu-Mitao and Kakimoto, 2014; Yu et al., 2013).

Besides a conserved F-box domain, TIR1 also contains a leucine-rich repeat (LRR) domain that is essential for its binding to AUX/IAA proteins (Gray et al., 1999; Tan et al., 2007). This observation was strengthened by identification of two point mutations in this domain of TIR1 (D170E and M473L), which increase the interaction of TIR1 with AUX/IAA proteins, resulting in their faster degradation and thus in enhanced transcription of auxin-responsive genes in the plant (Yu et al., 2013). The TIR1 and AFB protein family are encoded by six genes, and all of them are involved in auxin sensing to some extent (Dharmasiri et al., 2005b; Greenham et al., 2011). TIR1 and AFB2 are positive regulators of auxin signaling (Parry et al., 2009; Havens et al., 2012). There is evidence that AFB4 and AFB5 function as auxin receptors and their exact role still needs to be clarified; however, the role of AFB1 and AFB3 it this process is still not completely clear (Calderón Villalobos et al., 2010; Greenham et al., 2011; Parry et al., 2009; Walsh et al., 2006).

The AUX/IAA proteins are encoded by early auxin-responsive genes and act as transcriptional repressors in auxin responses (Mockaitis and Estelle, 2008). Most AUX/IAA proteins consist of four domains (Tiwari et al., 2001; Tiwari et al., 2004). It has been shown that domain II is important for recognition by TIR1 during auxin-induced destabilization of AUX/IAA proteins (Shimizu-Mitao and Kakimoto, 2014). Domains III and IV of AUX/IAA proteins share certain structural similarities with ARFs and contribute to homo- or hetero-dimerization within and between these two protein families (Guilfoyle and Hagen, 2012).

ARF transcription factors (a family of 23 members in *Arabidopsis*) contain a DNA-binding domain (DBD) that recognizes the auxin-response cis element (AuxRE) that is located in the promoter of auxin-responsive genes (Guilfoyle and Hagen, 2007; Ulmasov et al., 1997). Recently, a dimerization domain has been identified in the DBD that is necessary for the dimerization of ARFs; it is involved in ARF DNA binding and is essential for proper ARF function *in vivo* (Boer et al., 2014). At low auxin levels, AUX/IAA proteins are bound to ARFs and undergo heterotypic ARF–AUX/IAA interactions that are stronger and thus more favorable than homotypic ARF–ARF interactions. It appears that multiple AUX/IAA proteins might be required to efficiently repress the formation of an ARF-ARF dimer (Korasick et al., 2014, Nanao et al., 2014). The recruitment of the corepressor topless (TPL) and its associated chromatin-modifying machinery to this complex results in inhibition of transcription (Szemenyei et al., 2008; Tiwari et al., 2001).

Four different proteins participate in formation of the SCF^{TIR1} complex: TIR1, ring-box1 (RBX1), cullin 1 (CUL1), and *Arabidopsis* SKP1-like 1 (ASK1). The activity of the SCF^{TIR1} complex is regulated by covalent coupling of related to ubiquitin 1 (RUB1), a protein similar to ubiquitin, to the CUL1 subunit of SCF (del Pozo and Estelle, 1999). This process is coordinated by several other enzymes; of these, the most important is auxin-resistance 1 (AXR1). Modification of CUL1 by RUB1 appears to be highly important for SCF^{TIR1} activity and normal auxin responses (del Pozo et al., 2002). Mutations in the *AXR1* gene often result in an auxin-insensitive phenotype, such as reduced apical dominance, fewer lateral roots or reduced gravitropic response due to a decrease in the number of RUB1–CUL1 complexes (Lincoln et al., 1990; Leyser et al., 1993). Deconjugation of RUB1 from CUL1 also contributes to regulation of SCF^{TIR1} that is mediated by another enzymatic multiprotein complex, the COP9 signalosome (CSN) (Serino and Pick, 2013). Mutations in most of the CSN components confer auxin-resistant phenotypes to plants and result in defects in auxin-related developmental processes (del Pozo et al., 2002; Dharmasiri et al., 2003).

Cell-type-specific auxin responses might also be influenced by additional regulators of the SCF^{TIR1}–AUX/IAA–ARF pathway. For instance, TIR1 activity has recently been shown to be modulated by nitric-oxide-mediated S-nitrosylation, which leads to an increased TIR1–AUX/IAA interaction (Terrile et al., 2012). Recent reports show that the SCF^{TIR1}–AFB pathway is involved in degradation of PIN proteins and their vacuolar targeting (Baster et al., 2012), as well as links between auxin perception at the cell surface and the auxin signaling machinery in the nucleus (Tromas et al., 2013).

SKP2, an atypical auxin-binding protein

Involvement of both auxin receptor systems, ABP1 and TIR1/AFB–AUX/IAA, in the processes of auxin-dependent cell expansion and cell division has been observed (Schenck et al., 2010; Chen et al., 2001). The direct effect of the cell-surface-localized ABP1 on auxin-mediated cell cycle control suggested that there was a nuclear target (Braun et al., 2008), and SKP2 has been proposed as the potential downstream component that regulates the proteolysis of cell-cycle-related transcription factors. During the G1-to-S checkpoint in the cell cycle, some transcription factors and other proteins need to be degraded before the next phase can commence. SKP2, which is assumed to be a part of an SCF complex, participates in this process and so positively regulates cell cycle progression (Jurado et al., 2008). Of the two SKP2 genes in *Arabidopsis*, SKP2a can bind to auxin in cell-free assays and pulldown experiments, whereas SKP2b cannot (Jurado et al., 2010; Manzano et al., 2012). Binding of SKP2a to auxin enhances the interaction between SKP2a and the cell-division-related transcription factors EF2C and the protein dimerization partner of E2FB (DPB), which both are subsequently degraded, thus allowing cell cycle progression (see poster) (del Pozo et al., 2006; Jurado et al., 2008). In the *skp2* mutant, this interaction of SKP2 with transcription factors cannot occur, and EF2C and DPB accumulate in the cell. Although E2FB, another cell division transcription factor, is degraded in an SKP2-independent manner, E2FB is stabilized by auxin by an unknown mechanism (Jurado et al., 2010). Thus, besides the TIR1- or AFB-dependent auxin perception mechanism, SKP2 might provide an alternative pathway that contributes to the final response to auxin in the nucleus.

ABP1 is a crucial regulator of fast non-transcriptional responses

Since its original identification as a soluble 22-kDa large glycoprotein (Leblanc et al., 1997; Watanabe and Shimomura, 1998), ABP1 has been extensively studied as a candidate auxin receptor. The presence of the KDEL retention motif at its C-terminus suggests that ABP1 is predominantly localized in the ER, but a small fraction can also be found in the apoplast, the

Journal of Cell Science (2015) 128, 1–7 doi:10.1242/jcs.159418

extracellular space between the plasma membrane and the cell wall (Jones and Herman, 1993). Despite the fact that most of ABP1 is in the ER, the pH of the ER is not considered to be favorable for an auxin binding. The best environment for auxin binding, as experimentally proven, is at pH 5.5, which can be found in the apoplast, implying that ABP1 senses auxin at the cell surface (Jones and Herman, 1993; Diekmann et al., 1995; Tian et al., 1995; Leblanc et al., 1999, Woo et al., 2002). Early studies demonstrated that ABP1 is involved in the rapid regulation of membrane potential and ion fluxes at the plasma membrane and that it can positively control the auxin-induced cell swelling of *Arabidopsis* protoplasts and pea hypocotyls (Steffens et al., 2001; Yamagami et al., 2004). *ABP1* overexpression in tobacco (*Nicotiana tabacum*) plants causes only mild phenotypes, namely epinastic leaf curvature (Jones et al., 1998), but the *abp1*-knockout mutant has been reported to cause an embryonic-lethal phenotype (Chen et al., 2001). Heterozygous *abp1*/*ABP1* mutants also exhibit auxin-related defects, including root skewing, slightly elongated roots and hypocotyls, and apical dominance reduction, as well as decreased basipetal auxin transport (Effendi et al., 2011).

Measurements of auxin transport imply that ABP1 has an important role in the polarized auxin transport mechanism. It has been demonstrated that auxin-regulated retention of PIN1 and other cargos at the plasma membrane is mediated by ABP1 and is independent of the SCF^{TIR1} machinery (Paciorek et al., 2005; Robert et al., 2010). At low levels of cellular auxin, ABP1 reduces the cellular efflux of auxin by promoting PIN endocytosis. By contrast, at high auxin levels, auxin binds to ABP1 and inhibits endocytosis to stimulate auxin export from the cell (Čovanová et al., 2013; Nagawa et al., 2012). ABP1 positively regulates the recruitment of clathrin to the plasma membrane, which can be inhibited by auxin binding, leading to the reduced internalization of PIN proteins and enhanced auxin efflux. Auxin has been found to differentially regulate association of clathrin light chain (CLC) and clathrin heavy chain (CHC) with either the plasma membrane or the trans-Golgi network (TGN), or early endosomes, in a manner that depends on ABP1 and is independent of TIR1 or AFBs. In the presence of auxin, the association of CLC with the plasma membrane and TGN and early endosomes is reduced dramatically, while, at the same time, CHC begins to associate with these compartments (Robert et al., 2010; Wang et al., 2013).

The question of how ABP1 transmits the auxin signal from the cell surface to the cytosol in order to regulate different cellular processes had been an enigma for decades but was recently answered with the identification a transmembrane ABP1-interacting partner. The plasma membrane-localized transmembrane receptor-like kinase (TMK1) has been shown to interact with ABP1 in an auxin-dependent manner (see poster) (Dai et al., 2013; Xu et al., 2014). ABP1 and TMK1 form a cell surface auxin-sensing complex that activates known downstream players of the signaling pathway, such as the small GTPases of the Rho of plants family (ROPs) and their associated ROP-interactive CRIB motif-containing proteins (RICs) (Xu, et al., 2010; Chen et al., 2012). Auxin can activate both ROP2 and ROP6 within 30 seconds and can promote interdigitated growth of the epidermal pavement cells in *Arabidopsis* leaves leading to the formation of a variety of cell shapes, and, hence, a tissue resembling a jigsaw puzzle (see poster) (Xu et al., 2010). The ROP2–RIC4 and ROP6–RIC1 pairs act antagonistically on convex and concave sides of the lobes of pavement cells. ROP2–RIC4 stabilizes the actin cytoskeleton in the lobes (Fu et al., 2002), which reduces endocytosis of PIN1 and thereby promotes the localization of PIN1 to the plasma membrane in the lobes (Nagawa et al., 2012). By contrast, ROP6 loads RIC1 onto the microtubules, which inhibits exocytosis and so generates indentations (Fu et al., 2005). Once PIN1 is stabilized in the lobes, ABP1 senses the exported auxin and then acts through ROP6 in the opposite cell to form indentations there (Xu et al., 2010). In *Arabidopsis* roots, ABP1-activated ROP6–RIC1 recruits the microtubule-severing protein katanin (KTN1) during cortical microtubule rearrangement by promoting the detachment of branched microtubules (Lin et al., 2013). Through this mechanism, ROP6–RIC1 can regulate the association of clathrin with the plasma membrane for clathrin-mediated endocytosis (see poster) (Chen et al., 2012). Apart from endocytosis modulation, ROP1 through its partner interactor of constitutively active ROP1 (ICR1) can regulate PIN exocytosis (Lavy et al., 2007; Hazak et al., 2010). ICR1 can directly interact with subunit of exocyst complex SEC3A and thus control the exocytosis rate of PIN proteins (Lavy et al., 2007).

Although the majority of the effects of ABP1 mentioned above are related to non-transcriptional processes, there are some indications that ABP1 also influences auxin-regulated transcription. Conditional knockdown mutants of ABP1 have impaired regulation of cell elongation and cell division, and the mutants also display alterations in gene expression patterns in response to auxin (Braun et al., 2008; Tromas et al., 2009). The expression levels of some of the auxin-inducible genes, such as those of the AUX/IAA family, *SAUR* and *GH3*, are reduced in an ABP1-knockdown mutant and in the *abp1*/*ABP1* heterozygous mutant, suggesting that ABP1 can also affect the expression of auxin-responsive genes (Braun et al., 2008; Effendi et al., 2011). Active ROP (ROP-GTP) from tobacco expressed in *Arabidopsis* enhances the transcription rate of auxin-responsive genes, whereas expression of an inactive ROP (ROP-GDP) reduces gene transcription. This provides evidence that ROP-mediated signaling might act through the TIR1- or AFB-dependent AUX/IAA or SKP2a pathways to affect transcription (Tao et al., 2002). There is also some evidence that ABP1 might influence components that are involved in the G1-to-S transition, either independently of, or by acting through, SKP2a (Zažímalová et al., 2010). Interestingly, recent work indicates that ABP1 is also a negative regulator of the SCF^{TIR1}–AUX/IAA–ARF pathway (Tromas et al., 2013). ABP1 can counteract the phenotypes that are caused by the loss of the TIR1- or AFB-containing complex and, hence, is likely to genetically act upstream of these F-box proteins. Furthermore, knockdown of ABP1 also increases the degradation of AUX/IAA through the SCF^{TIR1} ubiquitin ligase pathway (Tromas et al., 2013). Moreover, an involvement of ABP1 in cell wall loosening and consequent cell expansion had already been described a decade ago (Steffens et al., 2001; Yamagami et al., 2004). Only recently, ABP1 has been found to control the expression of broad range of cell-wall-related genes, especially of those genes that mostly participate in cell wall remodeling, through a $SCF^{TIR1/AFB}$-dependent pathway. In particular, ABP1 plays a crucial role controlling the expression of genes involved in remodeling of xyloglucan side chains, which is an essential step for the spatial and temporal regulation of cell expansion (Paque et al., 2014). Recently, a connection between ABP1 and the phytochromes phyA and phyB has also been proposed. ABP1 negatively regulates phyB-dependent signaling, and thus hypocotyl elongation during shade avoidance syndrome

Journal of Cell Science (2015) 128, 1–7 doi:10.1242/jcs.159418

(Effendi et al., 2013). Taken together, these results suggest that auxin sensing at the cell surface might influence the sensitivity of the nuclear auxin receptors and, therefore, that ABP1 mediates not only non-transcriptional, but also transcriptional auxin responses.

Perspectives

In the past few years, the plant hormone field has made remarkable progress in understanding auxin perception and auxin signaling machineries. Despite the fact that our knowledge about individual signaling pathways has increased, there are crucial questions remaining to be solved. Among the most challenging are to identify the mechanisms that coordinate the different auxin perception systems and the machinery that regulates the various cellular processes that auxin is involved in, such as division and elongation.

Competing interests

The authors declare no competing interests.

Funding

This work was supported by the European Research Council [project ERC-2011-StG-20101109-PSDP]; European Social Fund [grant number CZ.1.07/2.3.00/20.0043] and the Czech Science Foundation GAČR [grant number GA13-40637S].

Cell science at a glance

A high-resolution version of the poster is available for downloading in the online version of this article at jcs.biologists.org. Individual poster panels are available as JPEG files at
http://jcs.biologists.org/lookup/suppl/doi:10.1242/jcs.159418/-/DC1.

References

Abas, L., Benjamins, R., Malenica, N., Paciorek, T., Wisniewska, J., Moulinier-Anzola, J. C., Sieberer, T., Friml, J. and Luschnig, C. (2006). Intracellular trafficking and proteolysis of the auxin efflux facilitator PIN2 in Arabidopsis is proteasome-dependent and involved in root gravitropism. *Nat. Cell Biol.* **8**, 249-256.

Barbez, E., Kubeš, M., Rolčík, J., Béziat, C., Pěnčík, A., Wang, B., Rosquete, M. R., Zhu, J., Dobrev, P. I., Lee, Y. et al. (2012). A novel putative auxin carrier family regulates intracellular auxin homeostasis in plants. *Nature* **485**, 119-122.

Baster, P., Robert, S., Kleine-Vehn, J., Vanneste, S., Kania, U., Grunewald, W., De Rybel, B., Beeckman, T. and Friml, J. (2012). SCF(TIR1/AFB)-auxin signalling regulates PIN vacuolar trafficking and auxin fluxes during root gravitropism. *EMBO J.* **32**, 260-274.

Benková, E., Michniewicz, M., Sauer, M., Teichmann, T., Seifertová, D., Jürgens, G. and Friml, J. (2003). Local, efflux-dependent auxin gradients as a common module for plant organ formation. *Cell* **115**, 591-602.

Bennett, M. J., Marchant, A., Green, H. G., May, S. T., Ward, S. P., Millner, P. A., Walker, A. R., Schulz, B. and Feldmann, K. A. (1996). Arabidopsis AUX1 gene: a permease-like regulator of root gravitropism. *Science* **273**, 948-950.

Blilou, I., Xu, J., Wildwater, M., Willemsen, V., Paponov, I., Friml, J., Heidstra, R., Aida, M., Palme, K. and Scheres, B. (2005). The PIN auxin efflux facilitator network controls growth and patterning in Arabidopsis roots. *Nature* **433**, 39-44.

Boer, D. R., Freire-Rios, A., van den Berg, W. A., Saaki, T., Manfield, I. W., Kepinski, S., López-Vidrieo, I., Franco-Zorrilla, J. M., de Vries, S. C., Solano, R. et al. (2014). Structural basis for DNA binding specificity by the auxin-dependent ARF transcription factors. *Cell* **156**, 577-589.

Braun, N., Wyrzykowska, J., Muller, P., David, K., Couch, D., Perrot-Rechenmann, C. and Fleming, A. J. (2008). Conditional repression of AUXIN BINDING PROTEIN1 reveals that it coordinates cell division and cell expansion during postembryonic shoot development in Arabidopsis and tobacco. *Plant Cell* **20**, 2746-2762.

Calderón Villalobos, L. I., Tan, X., Zheng, N. and Estelle, M. (2010). Auxin perception – structural insights. *Cold Spring Harb. Perspect. Biol.* **2**, a005546.

Calderón Villalobos, L. I., Lee, S., De Oliveira, C., Ivetac, A., Brandt, W., Armitage, L., Sheard, L. B., Tan, X., Parry, G., Mao, H. et al. (2012). A combinatorial TIR1/AFB-Aux/IAA co-receptor system for differential sensing of auxin. *Nat. Chem. Biol.* **8**, 477-485.

Chen, J. G., Ullah, H., Young, J. C., Sussman, M. R. and Jones, A. M. (2001). ABP1 is required for organized cell elongation and division in Arabidopsis embryogenesis. *Genes Dev.* **15**, 902-911.

Chen, X., Naramoto, S., Robert, S., Tejos, R., Löfke, C., Lin, D., Yang, Z. and Friml, J. (2012). ABP1 and ROP6 GTPase signaling regulate clathrin-mediated endocytosis in Arabidopsis roots. *Curr. Biol.* **22**, 1326-1332.

Cho, M., Lee, Z. W. and Cho, H. T. (2012). ATP-binding cassette B4, an auxin-efflux transporter, stably associates with the plasma membrane and shows distinctive intracellular trafficking from that of PIN-FORMED proteins. *Plant Physiol.* **159**, 642-654.

Čovanová, M., Sauer, M., Rychtář, J., Friml, J., Petrášek, J. and Zažímalová, E. (2013). Overexpression of the auxin binding protein1 modulates PIN-dependent auxin transport in tobacco cells. *PLoS ONE* **8**, e70050.

Dai, N., Wang, W., Patterson, S. E. and Bleecker, A. B. (2013). The TMK subfamily of receptor-like kinases in Arabidopsis display an essential role in growth and a reduced sensitivity to auxin. *PLoS ONE* **8**, e60990.

Dal Bosco, C., Dovzhenko, A., Liu, X., Woerner, N., Rensch, T., Eismann, M., Eimer, S., Hegermann, J., Paponov, I. A., Ruperti, B. et al. (2012). The endoplasmic reticulum localized PIN8 is a pollen-specific auxin carrier involved in intracellular auxin homeostasis. *Plant J.* **71**, 860-870.

del Pozo, J. C. and Estelle, M. (1999). The Arabidopsis cullin AtCUL1 is modified by the ubiquitin-related protein RUB1. *Proc. Natl. Acad. Sci. USA* **96**, 15342-15347.

del Pozo, J. C., Dharmasiri, S., Hellmann, H., Walker, L., Gray, W. M. and Estelle, M. (2002). AXR1-ECR1-dependent conjugation of RUB1 to the Arabidopsis Cullin AtCUL1 is required for auxin response. *Plant Cell* **14**, 421-433.

del Pozo, J. C., Diaz-Trivino, S., Cisneros, N. and Gutierrez, C. (2006). The balance between cell division and endoreplication depends on E2FC-DPB, transcription factors regulated by the ubiquitin-SCF^{SKP2A} pathway in Arabidopsis. *Plant Cell* **18**, 2224-2235.

Dharmasiri, S., Dharmasiri, N., Hellmann, H. and Estelle, M. (2003). The RUB/Nedd8 conjugation pathway is required for early development in Arabidopsis. *EMBO J.* **22**, 1762-1770.

Dharmasiri, N., Dharmasiri, S. and Estelle, M. (2005a). The F-box protein TIR1 is an auxin receptor. *Nature* **435**, 441-445.

Dharmasiri, N., Dharmasiri, S., Weijers, D., Lechner, E., Yamada, M., Hobbie, L., Ehrismann, J. S., Jürgens, G. and Estelle, M. (2005b). Plant development is regulated by a family of auxin receptor F box proteins. *Dev. Cell* **9**, 109-119.

Dhonukshe, P., Aniento, F., Hwang, I., Robinson, D. G., Mravec, J., Stierhof, Y. D. and Friml, J. (2007). Clathrin-mediated constitutive endocytosis of PIN auxin efflux carriers in Arabidopsis. *Curr. Biol.* **17**, 520-527.

Diekmann, W., Venis, M. A. and Robinson, D. G. (1995). Auxins induce clustering of the auxin-binding protein at the surface of maize coleoptile protoplasts. *Proc. Natl. Acad. Sci. USA* **92**, 3425-3429.

Ding, Z., Galván-Ampudia, C. S., Demarsy, E., Łangowski, Ł., Kleine-Vehn, J., Fan, Y., Morita, M. T., Tasaka, M., Fankhauser, C., Offringa, R. et al. (2011). Light-mediated polarization of the PIN3 auxin transporter for the phototropic response in Arabidopsis. *Nat. Cell Biol.* **13**, 447-452.

Ding, Z., Wang, B., Moreno, I., Dupláková, N., Simon, S., Carraro, N., Reemmer, J., Pěnčík, A., Chen, X., Tejos, R. et al. (2012). ER-localized auxin transporter PIN8 regulates auxin homeostasis and male gametophyte development in Arabidopsis. *Nat. Commun.* **3**, 941.

dos Santos Maraschin, F. S., Memelink, J. and Offringa, R. (2009). Auxin-induced, SCF(TIR1)-mediated poly-ubiquitination marks AUX/IAA proteins for degradation. *Plant J.* **59**, 100-109.

Effendi, Y., Rietz, S., Fischer, U. and Scherer, G. F. (2011). The heterozygous abp1/ABP1 insertional mutant has defects in functions requiring polar auxin transport and in regulation of early auxin-regulated genes. *Plant J.* **65**, 282-294.

Effendi, Y., Jones, A. M. and Scherer, G. F. (2013). AUXIN-BINDING-PROTEIN1 (ABP1) in phytochrome-B-controlled responses. *J. Exp. Bot.* **64**, 5065-5074.

Feraru, E., Vosolsobě, S., Feraru, M. I., Petrášek, J. and Kleine-Vehn, J. (2012). Evolution and structural diversification of PILS putative auxin carriers in plants. *Front. Plant Sci.* **3**, 227.

Friml, J., Benková, E., Blilou, I., Wisniewska, J., Hamann, T., Ljung, K., Woody, S., Sandberg, G., Scheres, B., Jürgens, G. et al. (2002). AtPIN4 mediates sink-driven auxin gradients and root patterning in Arabidopsis. *Cell* **108**, 661-673.

Friml, J., Vieten, A., Sauer, M., Weijers, D., Schwarz, H., Hamann, T., Offringa, R. and Jürgens, G. (2003). Efflux-dependent auxin gradients establish the apical-basal axis of Arabidopsis. *Nature* **426**, 147-153.

Fu, Y., Li, H. and Yang, Z. (2002). The ROP2 GTPase controls the formation of cortical fine F-actin and the early phase of directional cell expansion during Arabidopsis organogenesis. *Plant Cell* **14**, 777-794.

Fu, Y., Gu, Y., Zheng, Z., Wasteneys, G. and Yang, Z. (2005). Arabidopsis interdigitating cell growth requires two antagonistic pathways with opposing action on cell morphogenesis. *Cell* **120**, 687-700.

Ganguly, A., Sasayama, D. and Cho, H. T. (2012). Regulation of the polarity of protein trafficking by phosphorylation. *Mol. Cells* **33**, 423-430.

Geisler, M. and Murphy, A. S. (2006). The ABC of auxin transport: the role of p-glycoproteins in plant development. *FEBS Lett.* **580**, 1094-1102.

Geisler, M., Kolukisaoglu, H. U., Bouchard, R., Billion, K., Berger, J., Saal, B., Frangne, N., Koncz-Kalman, Z., Koncz, C., Dudler, R. et al. (2003). TWISTED DWARF1, a unique plasma membrane-anchored immunophilin-like protein, interacts with Arabidopsis multidrug resistance-like transporters AtPGP1 and AtPGP19. *Mol. Biol. Cell* **14**, 4238-4249.

Gray, W. M., del Pozo, J. C., Walker, L., Hobbie, L., Risseeuw, E., Banks, T., Crosby, W. L., Yang, M., Ma, H. and Estelle, M. (1999). Identification of an SCF ubiquitin-ligase complex required for auxin response in Arabidopsis thaliana. *Genes Dev.* **13**, 1678-1691.

Gray, W. M., Kepinski, S., Rouse, D., Leyser, O. and Estelle, M. (2001). Auxin regulates SCF(TIR1)-dependent degradation of AUX/IAA proteins. *Nature* **414**, 271-276.

Greenham, K., Santner, A., Castillejo, C., Mooney, S., Sairanen, I., Ljung, K. and Estelle, M. (2011). The AFB4 auxin receptor is a negative regulator of auxin signaling in seedlings. *Curr. Biol.* **21**, 520-525.
Grunewald, W. and Friml, J. (2010). The march of the PINs: developmental plasticity by dynamic polar targeting in plant cells. *EMBO J.* **29**, 2700-2714.
Guilfoyle, T. J. and Hagen, G. (2007). Auxin response factors. *Curr. Opin. Plant Biol.* **10**, 453-460.
Guilfoyle, T. J. and Hagen, G. (2012). Getting a grasp on domain III/IV responsible for Auxin Response Factor-IAA protein interactions. *Plant Sci.* **190**, 82-88.
Havens, K. A., Guseman, J. M., Jang, S. S., Pierre-Jerome, E., Bolten, N., Klavins, E. and Nemhauser, J. L. (2012). A synthetic approach reveals extensive tunability of auxin signaling. *Plant Physiol.* **160**, 135-142.
Hazak, O., Bloch, D., Poraty, L., Sternberg, H., Zhang, J., Friml, J. and Yalovsky, S. (2010). A rho scaffold integrates the secretory system with feedback mechanisms in regulation of auxin distribution. *PLoS Biol.* **8**, e1000282.
Jones, A. M. and Herman, E. M. (1993). KDEL-containing auxin-binding protein is secreted to the plasma membrane and cell wall. *Plant Physiol.* **101**, 595-606.
Jones, A. M., Im, K. H., Savka, M. A., Wu, M. J., DeWitt, N. G., Shillito, R. and Binns, A. N. (1998). Auxin-dependent cell expansion mediated by overexpressed auxin-binding protein 1. *Science* **282**, 1114-1117.
Jurado, S., Díaz-Triviño, S., Abraham, Z., Manzano, C., Gutierrez, C. and del Pozo, C. (2008). SKP2A, an F-box protein that regulates cell division, is degraded via the ubiquitin pathway. *Plant J.* **53**, 828-841.
Jurado, S., Abraham, Z., Manzano, C., López-Torrejón, G., Pacios, L. F. and Del Pozo, J. C. (2010). The Arabidopsis cell cycle F-box protein SKP2A binds to auxin. *Plant Cell* **22**, 3891-3904.
Kepinski, S. and Leyser, O. (2005). The Arabidopsis F-box protein TIR1 is an auxin receptor. *Nature* **435**, 446-451.
Kleine-Vehn, J. and Friml, J. (2008). Polar targeting and endocytic recycling in auxin-dependent plant development. *Annu. Rev. Cell Dev. Biol.* **24**, 447-473.
Kleine-Vehn, J., Dhonukshe, P., Sauer, M., Brewer, P. B., Wiśniewska, J., Paciorek, T., Benková, E. and Friml, J. (2008). ARF GEF-dependent transcytosis and polar delivery of PIN auxin carriers in Arabidopsis. *Curr. Biol.* **18**, 526-531.
Korasick, D. A., Westfall, C. S., Lee, S. G., Nanao, M. H., Dumas, R., Hagen, G., Guilfoyle, T. J., Jez, J. M. and Strader, L. C. (2014). Molecular basis for AUXIN RESPONSE FACTOR protein interaction and the control of auxin response repression. *Proc. Natl. Acad. Sci. USA* **111**, 5427-5432.
Lavy, M., Bloch, D., Hazak, O., Gutman, I., Poraty, L., Sorek, N., Sternberg, H. and Yalovsky, S. (2007). A novel ROP/RAC effector links cell polarity, root-meristem maintenance, and vesicle trafficking. *Curr. Biol.* **17**, 947-952.
Leblanc, N., Roux, C., Pradier, J. M. and Perrot-Rechenmann, C. (1997). Characterization of two cDNAs encoding auxin-binding proteins in Nicotiana tabacum. *Plant Mol. Biol.* **33**, 679-689.
Leblanc, N., David, K., Grosclaude, J., Pradier, J. M., Barbier-Brygoo, H., Labiau, S. and Perrot-Rechenmann, C. (1999). A novel immunological approach establishes that the auxin-binding protein, Nt-abp1, is an element involved in auxin signaling at the plasma membrane. *J. Biol. Chem.* **274**, 28314-28320.
Leyser, H. M., Lincoln, C. A., Timpte, C., Lammer, D., Turner, J. and Estelle, M. (1993). Arabidopsis auxin-resistance gene AXR1 encodes a protein related to ubiquitin-activating enzyme E1. *Nature* **364**, 161-164.
Lin, D., Cao, L., Zhou, Z., Zhu, L., Ehrhardt, D., Yang, Z. and Fu, Y. (2013). Rho GTPase signaling activates microtubule severing to promote microtubule ordering in Arabidopsis. *Curr. Biol.* **23**, 290-297.
Lincoln, C., Britton, J. H. and Estelle, M. (1990). Growth and development of the axr1 mutants of Arabidopsis. *Plant Cell* **2**, 1071-1080.
Ljung, K., Hull, A. K., Celenza, J., Yamada, M., Estelle, M., Normanly, J. and Sandberg, G. (2005). Sites and regulation of auxin biosynthesis in Arabidopsis roots. *Plant Cell* **17**, 1090-1104.
Manzano, C., Ramirez-Parra, E., Casimiro, I., Otero, S., Desvoyes, B., De Rybel, B., Beeckman, T., Casero, P., Gutierrez, C. and C Del Pozo, J. (2012). Auxin and epigenetic regulation of SKP2B, an F-box that represses lateral root formation. *Plant Physiol.* **160**, 749-762.
Michniewicz, M., Zago, M. K., Abas, L., Weijers, D., Schweighofer, A., Meskiene, I., Heisler, M. G., Ohno, C., Zhang, J., Huang, F. et al. (2007). Antagonistic regulation of PIN phosphorylation by PP2A and PINOID directs auxin flux. *Cell* **130**, 1044-1056.
Mockaitis, K. and Estelle, M. (2008). Auxin receptors and plant development: a new signaling paradigm. *Annu. Rev. Cell Dev. Biol.* **24**, 55-80.
Mravec, J., Skůpa, P., Bailly, A., Hoyerová, K., Krecek, P., Bielach, A., Petrásek, J., Zhang, J., Gaykova, V., Stierhof, Y. D. et al. (2009). Subcellular homeostasis of phytohormone auxin is mediated by the ER-localized PIN5 transporter. *Nature* **459**, 1136-1140.
Nagawa, S., Xu, T., Lin, D., Dhonukshe, P., Zhang, X., Friml, J., Scheres, B., Fu, Y. and Yang, Z. (2012). ROP GTPase-dependent actin microfilaments promote PIN1 polarization by localized inhibition of clathrin-dependent endocytosis. *PLoS Biol.* **10**, e1001299.
Nanao, M. H., Vinos-Poyo, T., Brunoud, G., Thévenon, E., Mazzoleni, M., Mast, D., Lainé, S., Wang, S., Hagen, G., Li, H. et al. (2014). Structural basis for oligomerization of auxin transcriptional regulators. *Nat. Commun.* **5**, 3617.
Naramoto, S., Kleine-Vehn, J., Robert, S., Fujimoto, M., Dainobu, T., Paciorek, T., Ueda, T., Nakano, A., Van Montagu, M. C., Fukuda, H. et al. (2010). ADP-ribosylation factor machinery mediates endocytosis in plant cells. *Proc. Natl. Acad. Sci. USA* **107**, 21890-21895.
Noh, B., Murphy, A. S. and Spalding, E. P. (2001). Multidrug resistance-like genes of Arabidopsis required for auxin transport and auxin-mediated development. *Plant Cell* **13**, 2441-2454.
Paciorek, T., Zažímalová, E., Ruthardt, N., Petrášek, J., Stierhof, Y. D., Kleine-Vehn, J., Morris, D. A., Emans, N., Jürgens, G., Geldner, N. and Friml J. (2005). Auxin inhibits endocytosis and promotes its own efflux from cells. *Nature* **435**, 1251-1256.
Paque, S., Mouille, G., Grandont, L., Alabadí, D., Gaertner, C., Goyallon, A., Muller, P., Primard-Brisset, C., Sormani, R., Blázquez, M. A. et al. (2014). AUXIN BINDING PROTEIN1 links cell wall remodeling, auxin signaling, and cell expansion in arabidopsis. *Plant Cell* **26**, 280-295.
Parry, G., Calderon-Villalobos, L. I., Prigge, M., Peret, B., Dharmasiri, S., Itoh, H., Lechner, E., Gray, W. M., Bennett, M. and Estelle, M. (2009). Complex regulation of the TIR1/AFB family of auxin receptors. *Proc. Natl. Acad. Sci. USA* **106**, 22540-22545.
Péret, B., Swarup, K., Ferguson, A., Seth, M., Yang, Y., Dhondt, S., James, N., Casimiro, I., Perry, P., Syed, A. et al. (2012). AUX/LAX genes encode a family of auxin influx transporters that perform distinct functions during Arabidopsis development. *Plant Cell* **24**, 2874-2885.
Petrášek, J., Mravec, J., Bouchard, R., Blakeslee, J. J., Abas, M., Seifertová, D., Wisniewska, J., Tadele, Z., Kubes, M., Covanová, M. et al. (2006). PIN proteins perform a rate-limiting function in cellular auxin efflux. *Science* **312**, 914-918.
Petroski, M. D. and Deshaies, R. J. (2005). Function and regulation of cullin-RING ubiquitin ligases. *Nat. Rev. Mol. Cell Biol.* **6**, 9-20.
Rakusová, H., Gallego-Bartolomé, J., Vanstraelen, M., Robert, H. S., Alabadí, D., Blázquez, M. A., Benková, E. and Friml, J. (2011). Polarization of PIN3-dependent auxin transport for hypocotyl gravitropic response in Arabidopsis thaliana. *Plant J.* **67**, 817-826.
Ranocha, P., Dima, O., Nagy, R., Felten, J., Corratgé-Faillie, C., Novák, O., Morreel, K., Lacombe, B., Martinez, Y., Pfrunder, S. et al. (2013). Arabidopsis WAT1 is a vacuolar auxin transport facilitator required for auxin homoeostasis. *Nat. Commun.* **4**, 2625.
Reinhardt, D., Pesce, E. R., Stieger, P., Mandel, T., Baltensperger, K., Bennett, M., Traas, J., Friml, J. and Kuhlemeier, C. (2003). Regulation of phyllotaxis by polar auxin transport. *Nature* **426**, 255-260.
Richter, S., Geldner, N., Schrader, J., Wolters, H., Stierhof, Y.-D., Rios, G., Koncz, C., Robinson, D. G. and Jürgens, G. (2007). Functional diversification of closely related ARF-GEFs in protein secretion and recycling. *Nature* **448**, 488-492.
Robert, S., Kleine-Vehn, J., Barbez, E., Sauer, M., Paciorek, T., Baster, P., Vanneste, S., Zhang, J., Simon, S., Čovanová, M. et al. (2010). ABP1 mediates auxin inhibition of clathrin-dependent endocytosis in Arabidopsis. *Cell* **143**, 111-121.
Rück, A., Palme, K., Venis, M. A., Napier, R. M. and Felle, H. H. (1993). Patch-clamp analysis establishes a role for an auxin binding protein in the auxin stimulation of plasma membrane current in Zea mays protoplasts. *Plant J.* **4**, 41-46.
Ruegger, M., Dewey, E., Hobbie, L., Brown, D., Bernasconi, P., Turner, J., Muday, G. and Estelle, M. (1997). Reduced naphthylphthalamic acid binding in the tir3 mutant of Arabidopsis is associated with a reduction in polar auxin transport and diverse morphological defects. *Plant Cell* **9**, 745-757.
Ruegger, M., Dewey, E., Gray, W. M., Hobbie, L., Turner, J. and Estelle, M. (1998). The TIR1 protein of Arabidopsis functions in auxin response and is related to human SKP2 and yeast grr1p. *Genes Dev.* **12**, 198-207.
Schenck, D., Christian, M., Jones, A. and Lüthen, H. (2010). Rapid auxin-induced cell expansion and gene expression: a four-decade-old question revisited. *Plant Physiol.* **152**, 1183-1185.
Serino, G. and Pick, E. (2013). Duplication and familial promiscuity within the proteasome lid and COP9 signalosome kin complexes. *Plant Sci.* **203-204**, 89-97.
Shimizu-Mitao, Y. and Kakimoto, T. (2014). Auxin sensitivities of all Arabidopsis Aux/IAAs for degradation in the presence of every TIR1/AFB. *Plant Cell Physiol.* **55**, 1450-1459.
Steffens, B., Feckler, C., Palme, K., Christian, M., Böttger, M. and Lüthen, H. (2001). The auxin signal for protoplast swelling is perceived by extracellular ABP1. *Plant J.* **27**, 591-599.
Swarup, R., Friml, J., Marchant, A., Ljung, K., Sandberg, G., Palme, K. and Bennett, M. (2001). Localization of the auxin permease AUX1 suggests two functionally distinct hormone transport pathways operate in the Arabidopsis root apex. *Genes Dev.* **15**, 2648-2653.
Swarup, K., Benková, E., Swarup, R., Casimiro, I., Péret, B., Yang, Y., Parry, G., Nielsen, E., De Smet, I., Vanneste, S. et al. (2008). The auxin influx carrier LAX3 promotes lateral root emergence. *Nat. Cell Biol.* **10**, 946-954.
Szemenyei, H., Hannon, M. and Long, J. A. (2008). TOPLESS mediates auxin-dependent transcriptional repression during Arabidopsis embryogenesis. *Science* **319**, 1384-1386.
Tan, X., Calderon-Villalobos, L. I., Sharon, M., Zheng, C., Robinson, C. V., Estelle, M. and Zheng, N. (2007). Mechanism of auxin perception by the TIR1 ubiquitin ligase. *Nature* **446**, 640-645.
Tanaka, H., Kitakura, S., De Rycke, R., De Groodt, R. and Friml, J. (2009). Fluorescence imaging-based screen identifies ARF GEF component of early endosomal trafficking. *Curr. Biol.* **19**, 391-397.

Journal of Cell Science

Tao, L. Z., Cheung, A. Y. and Wu, H. M. (2002). Plant Rac-like GTPases are activated by auxin and mediate auxin-responsive gene expression. *Plant Cell* **14**, 2745-2760.
Teh, O.-K. and Moore, I. (2007). An ARF-GEF acting at the Golgi and in selective endocytosis in polarized plant cells. *Nature* **448**, 493-496.
Terrile, M. C., París, R., Calderón-Villalobos, L. I., Iglesias, M. J., Lamattina, L., Estelle, M. and Casalongué, C. A. (2012). Nitric oxide influences auxin signaling through S-nitrosylation of the Arabidopsis TRANSPORT INHIBITOR RESPONSE 1 auxin receptor. *Plant J.* **70**, 492-500.
Tian, H., Klämbt, D. and Jones, A. M. (1995). Auxin-binding protein 1 does not bind auxin within the endoplasmic reticulum despite this being the predominant subcellular location for this hormone receptor. *J. Biol. Chem.* **270**, 26962-26969.
Tiwari, S. B., Wang, X. J., Hagen, G. and Guilfoyle, T. J. (2001). AUX/IAA proteins are active repressors, and their stability and activity are modulated by auxin. *Plant Cell* **13**, 2809-2822.
Tiwari, S. B., Hagen, G. and Guilfoyle, T. J. (2004). Aux/IAA proteins contain a potent transcriptional repression domain. *Plant Cell* **16**, 533-543.
Tromas, A., Braun, N., Muller, P., Khodus, T., Paponov, I. A., Palme, K., Ljung, K., Lee, J. Y., Benfey, P., Murray, J. A. et al. (2009). The AUXIN BINDING PROTEIN 1 is required for differential auxin responses mediating root growth. *PLoS ONE* **4**, e6648.
Tromas, A., Paque, S., Stierlé, V., Quettier, A. L., Muller, P., Lechner, E., Genschik, P. and Perrot-Rechenmann, C. (2013). Auxin-binding protein 1 is a negative regulator of the SCF(TIR1/AFB) pathway. *Nat. Commun.* **4**, 2496.
Ulmasov, T., Hagen, G. and Guilfoyle, T. J. (1997). ARF1, a transcription factor that binds to auxin response elements. *Science* **276**, 1865-1868.
Vanneste, S. and Friml, J. (2009). Auxin: a trigger for change in plant development. *Cell* **136**, 1005-1016.
Viaene, T., Delwiche, C. F., Rensing, S. A. and Friml, J. (2013). Origin and evolution of PIN auxin transporters in the green lineage. *Trends Plant Sci.* **18**, 5-10.
Walsh, T. A., Neal, R., Merlo, A. O., Honma, M., Hicks, G. R., Wolff, K., Matsumura, W. and Davies, J. P. (2006). Mutations in an auxin receptor homolog AFB5 and in SGT1b confer resistance to synthetic picolinate auxins and not to 2,4-dichlorophenoxyacetic acid or indole-3-acetic acid in Arabidopsis. *Plant Physiol.* **142**, 542-552.
Wang, C., Yan, X., Chen, Q., Jiang, N., Fu, W., Ma, B., Liu, J., Li, C., Bednarek, S. Y. and Pan, J. (2013). Clathrin light chains regulate clathrin-mediated trafficking, auxin signaling, and development in Arabidopsis. *Plant Cell* **25**, 499-516.
Watanabe, S. and Shimomura, S. (1998). Cloning and expression of two genes encoding auxin-binding proteins from tobacco. *Plant Mol. Biol.* **36**, 63-74.
Weijers, D., Sauer, M., Meurette, O., Friml, J., Ljung, K., Sandberg, G., Hooykaas, P. and Offringa, R. (2005). Maintenance of embryonic auxin distribution for apical-basal patterning by PIN-FORMED-dependent auxin transport in Arabidopsis. *Plant Cell* **17**, 2517-2526.
Wisniewska, J., Xu, J., Seifertová, D., Brewer, P. B., Ruzicka, K., Blilou, I., Rouquié, D., Benková, E., Scheres, B. and Friml, J. (2006). Polar PIN localization directs auxin flow in plants. *Science* **312**, 883.
Woo, E. J., Marshall, J., Bauly, J., Chen, J. G., Venis, M., Napier, R. M. and Pickersgill, R. W. (2002). Crystal structure of auxin-binding protein 1 in complex with auxin. *EMBO J.* **21**, 2877-2885.
Xu, T., Wen, M., Nagawa, S., Fu, Y., Chen, J. G., Wu, M. J., Perrot-Rechenmann, C., Friml, J., Jones, A. M. and Yang, Z. (2010). Cell surface- and rho GTPase-based auxin signaling controls cellular interdigitation in Arabidopsis. *Cell* **143**, 99-110.
Xu, T., Dai, N., Chen, J., Nagawa, S., Cao, M., Li, H., Zhou, Z., Chen, X., De Rycke, R., Rakusová, H. et al. (2014). Cell surface ABP1-TMK auxin-sensing complex activates ROP GTPase signaling. *Science* **343**, 1025-1028.
Yamagami, M., Haga, K., Napier, R. M. and Iino, M. (2004). Two distinct signaling pathways participate in auxin-induced swelling of pea epidermal protoplasts. *Plant Physiol.* **134**, 735-747.
Yu, H., Moss, B. L., Jang, S. S., Prigge, M., Klavins, E., Nemhauser, J. L. and Estelle, M. (2013). Mutations in the TIR1 auxin receptor that increase affinity for auxin/indole-3-acetic acid proteins result in auxin hypersensitivity. *Plant Physiol.* **162**, 295-303.
Zažímalová, E., Murphy, A. S., Yang, H., Hoyerová, K. and Hosek, P. (2010). Auxin transporters – why so many? *Cold Spring Harb. Perspect. Biol.* **2**, a001552.