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# Actin Dynamics in the Plant Cell

**Nella L. Klyachko**

Timiryazev Institute of Plant Physiology, Russian Academy of Sciences, Botanicheskaya str. 35, 127276 Moscow, Russia

*Correspondence*: **nellaklyachko@mtu-net.ru**

## ABSTRACT

Dynamic rearrangements of the actin cytoskeleton are one of the fastest responses of the plant cell to environmental signals and an important part of developmental programs. The turnover rate of actin microfilaments and supramolecular structures is several orders higher than that of actin proteins and mRNAs. The high rate of actin polymerization in the cell is provided by specific nucleating machineries, primarily by the Arp2/3 complex and formins. A wide set of actin-binding proteins capping, severing, cross-linking, and bundling actin filaments are involved in actin polymerization and depolymerization, accelerating these processes or protecting microfilaments against breakdown. The actin cytoskeleton is not only a target for various signals but also an effector for diverse physiological processes. Recently, some novel players in signaling to the plant actin cytoskeleton have been revealed, the WAVE complex and RIC proteins among them. The deciphering of signaling pathways from the actin cytoskeleton is only at the start. In this review, not all the relevant literature but mainly new developments in the field is summarized.

**Keywords:** actin, actin-binding proteins, filaments, lifetime, nucleators, signaling pathways, turnover
**Abbreviations: ABP**, actin-binding protein; **AIP**, actin-interacting protein; **ARP**, actin-related protein; **ADF,** actin-depolymerizing factor; **PCD**, programmed cell death; **$PIP_2$**, phosphatidylinositol 4,5-bisphosphate; **SI,** self-incompatibility

## CONTENTS



## INTRODUCTION

The dynamic actin cytoskeleton is important for numerous cellular functions, including cytoplasmic streaming, intracellular transport, cell division, cell shape creation and cell polarity determination, endocytosis and vesicle secretion, diverse metabolic processes, scaffolding the signaling pathways, organelle inheritance, etc.

Actin cytoskeleton remodeling occurs in response to various environmental and developmental cues, such as temperature, illumination, various stresses, pH changes, $Ca^{2+}$ concentration changes, pathogen attack, etc. In its turn, actin polymerization status and turnover rate can serve a signal for diverse cell responses.

The vast body of information concerning the topics in this field and daily appearing on the pages of scientific journals does not permit embracing it in the framework of this relatively short review. Therefore, only some basic positions and hot points will be highlighted. For more detail information I refer readers to a number of excellent recent reviews that cover related topics in greater depth (Wasteneys and Yang 2004; Smith and Oppenheimer 2005; Hussey *et al*. 2006; Moseley and Goode 2006; and numerous others partially listed below in the particular subsections of this review).

## VARIOUS LEVELS OF ACTIN TURNOVER

When speaking about actin turnover, we should distinguish G- and F-actin turnover. Both are controllable events but the range of the lifetime of these molecules differs considerably. G-actin is a very conservative globular protein comprising 375 amino acids, whose structure is presented in **Fig. 1**. It polymerizes into tightly helical filaments approximately 8 mm wide, which in their turn produce diverse higher-order structures within the cell.

Actin is one of the most stable proteins in the cell. Thus, the half-life of actin molecules within muscle sarcomers attains 20 days, although when the molecules abandon the filament, they may be destroyed within several minutes

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Invited Review

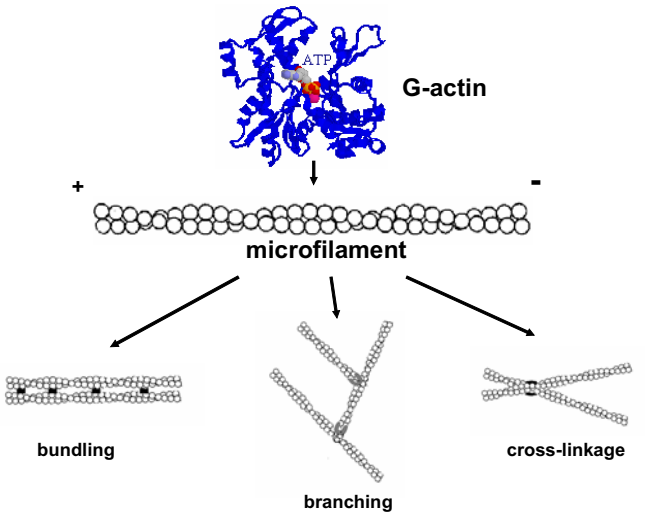


**Fig. 1 Structure of G-actin, F-actin, and some higher-order actin structures.** Actin monomer is a globular protein comprising four domains with a deep cleft between two of them, where the site of ATP binding is located. After G-actin polymerization, polar actin filaments are produced with rapidly growing barbed (+) and slowly growing pointed (-) ends. Diverse supramolecular actin structures are formed due to the activity of various actin-binding proteins.

(Russel *et al*. 2000). The half-life of β-actin mRNA in animal cells is from 5 to 14 h (Leclerc *et al*. 2002); the half-life of oat actin mRNA was estimated as 200 min (Byrne *et al*. 1963), i.e. this is a rather stable mRNA.

Actin synthesis could be controlled at the level of transcription; at least, the amount of particular actin isoforms could be changed due to the control of particular gene transcription. Thus, one of the Arabidopsis actin genes, *ACT7*, responded to auxin (2,4-D or IAA) treatment and other environmental stimuli, such as illumination or wounding (Kandasamy *et al*. 2001). Expression of the *ACT1* gene in malva (*Malva pusilla*) plants was first enhanced then sharply suppressed by plant infection with the fungus *Colletotrichum gloeosporioides* (Jin *et al*. 1999). However, the total level of actin mRNA does not usually change dramatically under physiological conditions and does this usually in parallel with the growth rate and the total RNA amount, which underlies the commonly accepted usage of this mRNA as a loading control in blotting experiments.

The total amount of actin protein in various plant tissues could vary by 100 times. In some cells, maize pollen for example, actin could comprise up to 20% of total protein (Liu and Yen 1992). The amount of actin mRNA and protein increased five-fold during germination of common bean seeds (Villanueva *et al*. 1999) and somewhat less during germination of maize seeds (Diaz-Camino *et al*. 2004). However, these changes were very slow processes, which became apparent only after several days of germination.

In contrast, the relative level of actin filaments and actin-based high-order structures is one on the fastest cell responses to constantly changing extracellular and intracellular signals, which play an important role in numerous cellular processes.

Thus, the lifetime of actin filaments in the "comet tails" of the enteropathogenic bacteria propelling within and between infected animal cells, such as *Listeria monocytogene*, *Shigella flexneri*, and *Rickettsia rickettsii* varied from 30 to 100 s (reviewed in Fehrenbacher *et al*. 2003).

The lifetime of actin patches in budding yeast was approximately 10 to 20 s, and the lifetime of actin cables was 1 to 2 min (reviewed in Moseley and Goode 2006).

In cultured mast cells, endocytic vesicles were propelled from the plasma membrane into the cytosol by "comet tails" of rapidly polymerizing actin, whose turnover occurred at the rate of 20 s (Merrifield *et al*. 1999).

Within a period from 30 s to 2 min after self-incompatibility signaling, reorganization and depolymerization of filamentous actin was induced in field poppy pollen tubes (Geitmann *et al*. 2000; Snowman *et al*. 2002).

Rapid oscillations of actin polymerization/depolymerization occur in the tips of growing pollen tubes (e.g. Lovy-Wheeler *et al*. 2006).

The rate of actin filament turnover *in vivo*, for example in human leukocytes, was ~100-fold faster than that of filaments assembled from purified actin *in vitro* (Zigmond 1993), indicating that cells harbor factors that strongly promote turnover. Among these factors are actin nucleators and diverse actin-binding proteins (ABPs) functioning in concert and inducing different effects in dependence on their combinations (see below).

The cell contains functionally distinct actin pools of varying stability. Some filaments are more stable than others within a single cell, being protected by side-binding, bundling, and cross-linking proteins (Kovar *et al*. 2000; Huang *et al*. 2005; Thomas *et al*. 2006) and destabilized by other ABPs or by actin phosphorylation (Liu *et al*. 2006). For example, treatment of growing lily pollen tubes with actin-depolymerizing drugs or their rapid acidification resulted in the disappearance of the subapical F-actin fringe within several seconds, whereas actin cables continued to maintain cytoplasmic streaming (Vidali *et al*. 2001; Lovy-Wheeler *et al*. 2006).

Thus, the turnover rate of actin microfilament and actin-based supramolecular structures is several orders higher than that of actin proteins and mRNAs, and just this high dynamicity permits the cell to respond quickly to changing environmental conditions.

## MICROFILAMENT POLYMERIZATION/DEPOLYMERIZATION

The nucleation process is the rate-limiting step for actin assembly, which is determined by the rate of polymerization of the first two or three monomers. Spontaneous actin polymerization *in vitro* has a relatively long lag period required for correct assembly of these first monomers. In addition, spontaneous polymerization demands a rather high concentration of actin monomer presence. In the living cell, most actin monomers are not free but sequestered by profilin and special nucleating complexes bypassing kinetic barriers to actin assembly are involved in actin polymerization.

### The Arp2/3 complex

One such complex is the Arp2/3 complex (reviewed in Borisy and Svitkina 2000; Smith and Oppenheimer 2005; Hussey *et al*. 2006; and many others). It was firstly identified in *Acanthamoeba* (Machesky *et al*. 1994) and appears to be conserved in all eukaryotes (Machesky and Gould 1999). In particular, all components of this complex were identified in the Arabidopsis genome and detected in the zones of cell active growth. Mutations in each of its components resulted in morphological defects (Mathur *et al*. 2003a, 2003b; Harris *et al*. 2005).

The Arp2/3 complex is composed of seven subunits: Arp2 and Arp3, belonging to the family of actin-related proteins (ARPs), and five novel proteins called ArpC1–ArpC5 (Winder 2003).

The Arp2/3 complex can bind to the sides of actin filaments. At the side of a "mother" filament, the Arp2/3 complex will nucleate a new "daughter" filament at an angle of 70° (Mullins *et al*. 1998).

The higher-order organization of Arp2/3-dependent actin filament networks depends on the balanced activity of additional ABPs, preferentially providing for so-called dendritic polymerization but generating long bundles of aligned actin filaments as well.

Branched actin filaments are often located near the membrane of the leading edge of motile animal cells, and just actin polymerization creates a force pushing this membrane (Borisy and Svitkina 2000). Rapid actin polymerization by the activated Arp2/3 complex is also the basis for

intracellular motility of some enteropathogenic bacteria within and between animal cells, for endosome movements in yeast and animal cells, and maybe for mitochondria transport (reviewed in Fehrenbacher *et al*. 2003).

In plants, this mechanism of actin polymerization evidently plays a substantially less important role than in animals and yeast. In fact, loss-of-function mutations in individual subunits of this complex are lethal in single-celled organisms, such as *Saccharomyces cerevisiae* (Winter *et al*. 1999), as well as in multicellular eukaryotes, such as *Caenorhabditis elegans* (Sawa *et al*. 2003) or *Drosophila* (Hudson and Cooley 2002), whereas they result in relatively small defects in only some plant tissues (Mathur *et al*. 2003a, 2003b; Harris *et al*. 2005).

The Arp2/3 complex by itself is inactive; it needs activation for rapid actin nucleation. Diverse mechanisms of this activation are described (see below). For activation, structural rearrangement of the complex is required: Arp2 and Arp3 subunits should be brought closer together to nucleate actin. Some inhibitors of the Arp2/3 complex nucleating activity are also known.

## Formins

Other actin nucleators are formins (reviewed in Evangelista *et al*. 2003; Higgs 2005; and others). All formins contain a unique, highly conserved so-called formin homology domain (FH2) that interacts with actin, as well as a proline-rich domain (FH1) that binds to profilin, the actin monomer-binding protein. The mechanism of formin-induced actin filament nucleation is quite different to than that of the Arp2/3 complex. Formin is a capping protein, which, distinct from the Arp2/3 complex, attaches to the growing barbed actin filament end. Its FH2 domain can produce a dimer stabilizing the first two actin monomers, thus creating the nucleus for further polymerization. Formins are so-called leaky or processive cap proteins, which remain to be bound to the growing barbed filament end but permit the attachment of new actin monomers to it, i.e. filament elongation. At the same time, they prevent the attachment of other tight-capping proteins. As a result, very long unbranched filaments are produced. Further activity of bundling ABPs provides for thick actin cable formation. Formin FH1 proline-rich domain binds in an actin-profilin complex, thus permitting for the efficient use of this complex (representing a dominating pool of actin in the cell) for actin polymerization.

Formins are found in a wide range of species, plant species in particular. In Arabidopsis, 21 genes for formin-like proteins were identified (Deeks *et al*. 2002). Two classes of plant formins were found, one of which is specific for plants, being an integral membrane protein, as distinct from cytoplasmic or nuclear formins of other organisms (Cvrčková 2000). In addition, plant formins are devoid of a small GTPase-binding domain and evidently are not the components of the Rop GTPase signaling pathways (see below).

## Other actin-binding proteins as modulators of actin filament dynamics

The dynamic nature of the actin cytoskeleton is conferred by a number of ABPs that bind to and cross-link actin filaments, bundle filaments together, sever actin filaments, cap the ends of filaments, or bind to actin monomers. Several plant ABPs have also been isolated and characterized (reviewed in Pollard and Cooper 1986; Staiger and Hussey 2004; Wasteneys and Yang 2004; Hussey *et al*. 2006, and others), and the list of plant ABPs affecting actin turnover is constantly increasing (Fan *et al*. 2004; Thomas *et al*. 2006).

### *Profilin*

Profilins are small ubiquitous proteins widely distributed in plants and animals. In Arabidopsis, five profilins were identified, three of them being expressed in vegetative organs and two mainly expressed in pollen.

Profilins interact with actin monomers, and this could differently affect actin polymerization. On the one hand, most actin monomers in the living cell are not free but sequestered by profilin, which prevents their spontaneous polymerization. The actin-profilin complex could not be attached to the filament pointed ends. On the other hand, the complex of actin and profilin could be efficiently used by specific nucleation machineries. Thus, actin nucleators comprise profilin-binding domains (for example, proline-rich FH1 domains of formins), and binding the actin-profilin complex to these domains could increase local G-actin concentration near the filament barbed ends. In addition, profilin could carry an actin monomer to this site in a correct orientation relative to the growing filament. Therefore, in the presence of formins, profilin accelerates actin polymerization (Yi *et al*. 2005). Profilin could also interact with polyphosphoinositides, releasing free G-actin, which increases the local polyphosphoinositide pool near the plasma membrane, thus affecting other mechanisms of actin polymerization.

Profilins are found in both the cytosol and nucleus, demonstrating that they could manifest multifaceted activity, for example, via binding to transcription factors and affecting gene expression (Lederer *et al*. 2005). However, it is not clear whether this activity is related to its more well-studied action on actin dynamics.

### *ADF/cofilin and AIP*

Controlled F-actin depolymerization is as important for actin turnover as its polymerization. Cofilin and gelsolin are two basic ABPs accelerating filament degradation.

Actin-depolymerizing factor (ADF)/cofilin is a small ubiquitous protein that binds to both G- and F-actin. It enhances the rate of monomer dissociation from the pointed end of actin filaments and severs actin filaments (reviewed in Bamburg 1999; des Marais *et al*. 2005; Hussey *et al*. 2006; Mohri *et al*. 2006). Its severing activity is related to ADF capability of twisting actin filaments, thus weakening monomer interaction and inducing filament fragmentation.

The activity of ADF/cofilin is regulated by several mechanisms, including phosphorylation/dephosphorylation (of some of them), pH, phosphoinositides, and competition with other actin-binding proteins (Allwood *et al*. 2002). Phosphorylation of Ser-6 by a calmodulin-like domain protein kinase suppresses severing and depolymerizing activities of plant ADF. ADF preferentially binds with F-actin at pH 6.0 and severs actin filaments at pH > 7.4. Binding to phosphatidylinositol 4,5-bisphosphate ($PIP_2$) or phosphatidylinositol 4-monophosphate decreases ADF activity. As distinct from animal cells, in plant cells ADF is often localized along F-actin filaments because it manifests a relatively weaker severing activity.

Actin-interacting protein (AIP) enhances fragmentation of ADF/cofilin-bound filaments and caps the barbed ends (reviewed in Ono 2003). It was proposed that short F-actin fragments produced by ADF severing activity could not anneal and depolymerize rapidly from the pointed ends. However, this supposition was later questioned (Ono *et al*. 2004). Cooperative activity of ADF and AIP1 proteins in actin filament severing is related to AIP1 direct binding to ADF across the cleft between the two propeller domains and to actin via two binding sites in both propeller domains flanking the ADF-binding site (Clark *et al*. 2006).

The efficiency of ADF + AIP severing activity depends on their balance with other ABPs. In animal and yeast cells, ADF/cofilin competes with tropomyosin, a protein that binds along the sides of actin filaments, for binding with actin filament; the latter protect filaments from severing. Proteins that cross-link actin into stable structures may also protect actin filaments against branching and severing.

Within the cells, ADF and AIP locate mainly in the sites of rapid actin polymerization, for example, in tip regions of

root hairs and pollen tubes. Overexpression of Arabidopsis ADF (AtADF1) resulted in the disappearance of thick actin cables and reduced the growth of cells and organs. In contrast, suppressed ADF expression promoted the formation of actin cables and stimulated cell expansion as well as organ growth (Dong *et al*. 2001). In Arabidopsis, the reduction of AIP1 expression by $RNA_i$ was correlated with reduced leaf and plant size (Ketelaar *et al*. 2004).

#### *Gelsolin*

Gelsolin is a calcium-regulated actin filament severing, nucleating, and barbed end capping factor. Recently, a gelsolin-like 80-kD protein was isolated from *Papaver rhoeas* pollen tubes and characterized (Huang *et al*. 2004). The gelsolin molecule comprises six specific so-called gelsolin repeats. Its involvement in rapid actin depolymerization during self-incompatibility response of poppy plants was supposed (Huang *et al*. 2004).

#### *Bundling, capping, and some other actin-binding proteins*

Bundling proteins increase bundle thickness and, as a rule, filament stability. In plants, villin and fimbrin were found, each of them being encoded by a 5-member gene family in *Arabidopsis thaliana*. Villin structure has much in common with gelsolin, but villins have one more gelsolin repeat; at the same time, villins and gelsolin fulfill different functions. Two actin-bundling proteins from lily (*Lilium longiflorum*) pollen tubes, 135-ABP and 115-ABP, were isolated and identified as plant villins. They arrange F-actin filaments with uniform polarity into bundles in a Ca-dependent mode (Yokota *et al*. 1998, 2003). One more but calcium-independent villin (VLN1) was isolated from Arabidopsis, which increased actin bundle resistance to ADF-mediated depolymerization (Huang *et al*. 2005).

Arabidopsis fimbrin also stabilized actin filaments against profilin-mediated depolymerization *in vitro* and *in vivo* (Kovar *et al*. 2000).

Recently, a novel plant ABP WLIM1 was found in tobacco plants, which stimulated actin filament bundling, thus increasing their stability (Thomas *et al*. 2006).

Among other ABPs identified in plants are capping proteins, whose concentration determines the length of actin filaments (Huang *et al*. 2003), cyclase associated protein (CAP), a bifunctional protein binding monomeric actin in various organisms (reviewed in Hubberstay and Mottillo 2002), which was found in cotton and Arabidopsis plants (its overexpression resulted in the loss of actin filaments and induced morphogenetic defects (Barrero *et al*. 2002) and in *Dictyostellium* cells, where it controlled cell polarity and cAMP signaling (Noegel *et al*. 2004). Some ABPs could be simultaneously associated with microtubules, thus providing for the interconnection and functional cooperation between the two cytoskeletal systems (Igarashi *et al*. 2000; Preuss *et al*. 2004).

The potential activities of many ABPs were studied by *in vitro* assays, but *in vivo* they might be functionally different. In the cell, their activities are restricted by other ABPs, for example, by competing for the sites of binding to microfilaments. Thus, whether ADF severing results in filament assembly or disassembly *in vivo* depends on whether the newly generated barbed ends are capped. The balance between different ABPs will dictate a dominant response. Regretfully, cellular functions of some plant ABPs are not yet clearly elucidated.

## SIGNALING TO AND FROM THE ACTIN CYTOSKELETON

### To the actin cytoskeleton

Actin cytoskeleton is simultaneously a target and effector for diverse signaling cascades (**Fig. 2**). Signaling to the actin cytoskeleton is considered in many comprehensive reviews (Schmidt and Hall 1998; Staiger 2000; Drøbak *et al*. 2003; Šamaj *et al*. 2004a; and many others), whereas the examination of actin functioning as an effector of physiological processes is only at the start.

Small GTPases play a central and integral role in mediating the action of diverse signals inducing remodeling the actin cytoskeleton in yeast, animals, and plants. Signal plant GTPases are a specific class of so-called Rop GTPases differing from other eukaryotic small GTPases (Rho, Rac, and Cdc42) (Yang 2002). The Arabidopsis genome comprises 11 and the maize genome 9 genes for Rop GTPases. They can be in an inactive GDP-bound or active GTP-bound form. Active small GTPases are located in the plasmalemmal microdomains in the regions of rapid growth, e.g. in the tips of the root hairs and pollen tubes or in the growing lobes of the epidermal pavement cells (Molendijk *et al*. 2001; Fu *et al*. 2002; Gu *et al*. 2003, 2005). In the dominant-negative and constitutively active mutants with the decreased or increased amount of active Rop GTPases forms, respectively, growth disturbances were observed.

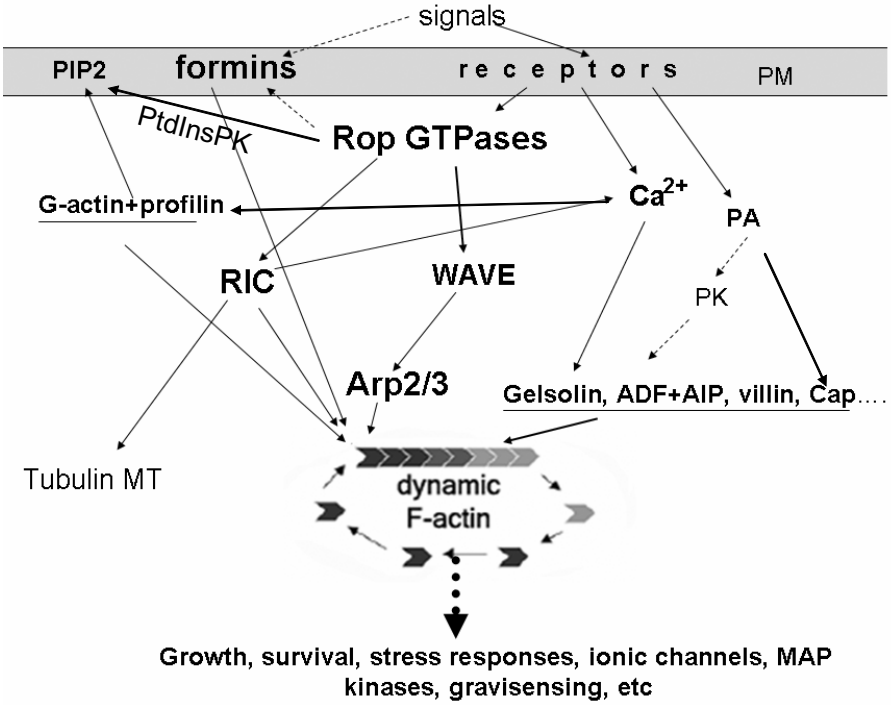


**Fig. 2 Scheme of critical signaling pathways controlling actin cytoskeleton dynamics in the plant cell.** ADF, actin depolymerizing factor; AIP, actin-interacting protein; Cap, capping proteins; PA, phosphatidic acid; PIP2, phosphatidylinositol 4,5-bisphosphate; PK, protein kinases; PM, plasma membrane; PtdInsPK, phosphatidylinositol monophosphate kinase. Dashed lines designate the pathways, whose occurrence is only supposed and molecular linkers are not known.

Several downstream target proteins for small GTPase signaling are described. In animal cells, signaling to the Arp2/3 complex is mediated by an autoinhibitory WASP, SCAR/WAVE complex (Suppressor of cAMP Receptor from *Dictyostelium*/WASP family Verprolin homologous protein), VASP, formins, and some other proteins. In plants, until recently no intermediates in the Rop signaling to Arp2/3 complex were detected. However, now it is believed that the WAVE complex evidently functions in plants as well.

The WAVE complex comprises five subunits: SCAR/WAVE, NAP1, HSPC300, Abi, and PIRI21, and homologues of all these subunits were found in the Arabidopsis genome (terminology of these proteins is not yet established, and each of these proteins has other names, for example BRK1 and SRA1 are Arabidopsis homologues of HSPC300 and PIR121, respectively). The WAVE complex interacts physically with the small GTPase via PIR121 subunit and with the Arp2/3 complex via the C-end of the WAVE subunit.

The WAVE complex needs to be activated to fulfill its second messenger functions. There are several hypotheses explaining WAVE complex activation. According to one of them, a SCAR/WAVE subunit is inactive within the WAVE complex and can interact with Arp2/3 only after release from this complex (Gautreau *et al*. 2004). According to another hypothesis, WAVE complex activation occurs due to its re-localization and bringing it closer to the Arp2/3 complex (Innocenti *et al*. 2004).

Mutations in various subunits of the WAVE complex resulted in similar, although less pronounced, morphological defects as mutations in the Arp2/3 complex, indicating that both complexes are the elements of the same signaling pathway (Mathur *et al*. 2003a, 2003b; Szymanski 2005; Zhang *et al*. 2005).

Other small GTPase targets in animal cells are formins. In contrast, plant formins lack domains for direct interacttion with GTPases. Moreover, plant-specific group 1 formins harbor extracellular and transmembrane domains, thus serving as perfect candidates for mediating extracellular stimulus direct effects on the actin cytoskeleton (Cvrćková 2000; Deeks *et al*. 2005). Alternatively, some so far unknown second messengers function between Rop GTPases and formins.

One more recently highlighted Rop-dependent pathway of the action on the actin cytoskeleton is a signal transduction via so-called RIC proteins (Rop-interacting proteins containing CRIB sequence interacting with the effector domain of Cdc42/Rac GTPases in animals) (Wu *et al*. 2001). Specific Rop-RIC pairs act in distinct Rop signaling pathways, which are not necessary related directly to cytoskeleton remodeling. Thus, Rop1 GTPase located in the plasma membrane in the tip of the growing tobacco pollen tube interacts with two proteins, one of which (RIC3) controls a periodic calcium ion uptake by the pollen tube tip and another (RIC4) regulates a dynamics of actin microfilaments in this region (Gu *et al*. 2005). Another pair of RIC proteins, RIC1 and RIC4, is a target of Rop2 GTPase affecting two cytoskeletal components, microtubules and microfilaments, in pavement cells of the Arabidopsis epidermis (Fu *et al*. 2005). Thus, this pair of ROP effectors can coordinate activities of the two cytoskeletal systems. In this case, RIC1 protein is a microtubule-associated protein, which can directly affect the tubulin cytoskeleton, whereas the downstream elements for RIC4 action on the actin cytoskeleton are so far unknown.

Phosphatidylinositol monophosphate kinase (PtdInsPK) is one more effector of small GTPases, whereas $PIP_2$, the product of its activity, can bind some ABPs, profilin in particular, thus affecting actin polymerization (Kost *et al*. 1999). Location of $PIP_2$ in definite membrane domains can serve as a basis for local actin rearrangements within the cell.

Although Rop GTPases are the central component of several signaling pathways to the actin cytoskeleton, they are not the only ones. Some other integral signaling agents are described. Among them are $Ca^{2+}$, inositol phospholipids, protein kinases, protein phosphatases, cyclic mononucleotides, etc).

The calcium signal mediated by some ABPs, profilin and gelsolin in particular, can result in actin cytoskeleton degradation. Such Ca-dependent degradation of the cytoskeleton was observed, for example, in response to the signal of self-incompatibility in *Papaver rhoeas* pollen tubes (Staiger and Franklin-Tong 2003). In this case, the concentration of cytosolic $Ca^{2+}$ increased within a few seconds, indicating that it was one of the first second messengers in this process. A tight connection between actin cytoskeleton organization and steep tip-focused $Ca^{2+}$ gradients in tip-growing cells is well known.

Phosphoinosite phosphatases are required for normal actin organization in elongating cells of the Arabidopsis inflorescence (Zhong *et al*. 2004, 2005). Mitogen-activated protein kinases (MAPKs) are also involved in actin cytoskeleton remodeling (Šamaj *et al*. 2002, 2004a).

Phosphatidic acid (PA) mediates plant responses to osmotic stress, wounding, and phytohormones. Lee *et al*. (2003) showed that the addition of PA to soybean cell suspension increased the level of filamentous actin in them three- to four-fold within 30 min. The authors supposed the involvement of protein kinases in PA downstream signaling. In Arabidopsis, actin heterodimering capping protein (AtCP) interfering with actin polymerization is among PA effectors (Huang *et al*. 2006). Treatment with PA of Arabidopsis suspension cells and poppy pollen grains elevated the level of filamentous actin substantially.

## From the actin cytoskeleton

Thus, a complicated network of signaling pathways is involved in actin cytoskeleton reorganization in response to diverse extracellular and intracellular signals. In its turn, the actin cytoskeleton polymerization status can serve as a signal for numerous physiological processes. Actin could not only receive signals but also transduce them, thus determining cellular responses.

Direct or indirect effects of actin on gene transcription in the plant cell are essentially unknown. However, actin, myosins, and ARPs were detected in the interphase nuclei of eukaryotes, plants in particular (Lanerolle and Cole 2002; Paves and Truve 2004), but the function of nuclear actin is yet undefined. Its structural role seems most probable. ARPs are the components of multiprotein chromatin-remodeling complexes involved in chromatin-mediated gene regulation, in particular genes controlling flowering (Kandasamy *et al*. 2004, 2005; Martin-Trillo *et al*. 2006). ABPs, tobacco WLIM1, for example, were also detected in nuclei (Thomas *et al*. 2006), indicating their putative nuclear functions. These functions are not so far identified. However, Kawaoka *et al*. (2000) reported that this protein affected the *cis*-acting element for several phenylpropanoid synthetic genes.

The signal source could be the level of polymerized actin, the ratio of polymeric to monomeric actin, the tensional changes within the actin network, or the rate of actin turnover. Scarce accumulated information favors the last. Pharmacological analysis can help to distinguish between actin level and actin turnover signals. For example, actin-stabilizing drugs, such as jasplakinolide or phalloidin, reduce actin dynamics without a reduction in the amount of F-actin. However, artificial actin filament stabilization with specific drugs might evidently exert other effects than natural actin filament stability. Other ways of artificial changing the rate of actin turnover are some actin mutations or deletions of genes for actin-bundling proteins stabilizing actin microfilaments.

In yeast, it is believed that cell survival depends on the rate of actin dynamics but not on the actin level: the reduced rate of actin dynamics was correlated with the increased ROS level and accelerated cell death along the apoptotic pathway (Gourlay and Ayscough 2005). As distinct from

yeast cells and like some mammalian cells, in self-incompatible (SI) poppy pollen tubes, not only actin stabilization but even short-term actin depolymerization induced by the SI signal or latrunculin B triggered programmed cell death (PCD), and jasplakinolide-induced actin stabilization neutralized this effect (Thomas *et al*. 2006). These actin-based signals were sufficient for PCD induction.

Actin can exert indirect effects by affecting ionic channels and triggering corresponding signaling pathways. For example, actin filaments were shown to modulate inward $K^+$ channels in stomatal guard cells (Hwang *et al*. 1997; Liu and Luan 1998). The actin-based modulation of channel functions was shown to depend on actin dynamics near the animal cell membrane rather than on the presence of preformed filamentous actin (Shumilina *et al*. 2003). Regretfully, there is no similar reliable data for plant cells.

Pharmacological actin stabilization inhibited or prevented, whereas actin disintegration promoted root gravibending (Hou *et al*. 2003; Mancuso *et al*. 2006), indicating the role of a rapid actin turnover in the graviresponse (Hou *et al*. 2003; Mancuso *et al*. 2006).

Both actin depolymerization by latrunculin B and its stabilization by jasplakinolide activated stress-induced MAPK in alfalfa root-derived cell culture (Šamaj *et al*. 2002). Latrunculin B activated whereas jasplakinolide inhibited alfalfa stress-activated MAPK, thus mimicking structural changes in the plasma membrane translated via the actin cytoskeleton (Sangwan *et al*. 2002).

It is often difficult to distinguish between actin cytoskeleton as a signaling agent, the scaffold for other signaling pathways, or the track for signaling molecule movement. However, even in the latter case, some selectivity in such transport was suggested to be a possible mechanism for actin signaling, for example, selective transport of newly formed mitochondria into yeast buds with retaining old, damaged mitochondria, a source of PCD signals, in the mother cell (Gourlay and Ayscough 2005). Another example is an endocytosis of vesicles carrying the components of signaling pathways and favoring signal dispersion within the cell (Šamaj *et al*. 2004b) or actin influence on the distribution of ionic channels due to changes in the transport of channel protein-bearing vesicles (Levina *et al*. 1994).

Thus, actin is not a final but an intermediary element of many signaling pathways in the cell. The highly dynamic state of the actin cytoskeleton is characteristic of a healthy cell and a sensor of various stresses. The cells with reduced actin turnover lack a possibility of a rapid response to changing environmental conditions.

## CONCLUDING REMARKS

The actin cytoskeleton is a key element in the plant's response to various environmental and intracellular signals. Its turnover within the plant cell is not only a target but also an effector of diverse cellular processes. Considerable progress has been made during the last decade with respect of the mechanisms involved. Actin nucleating machineries and ABPs involved in actin dynamic rearrangements were characterized; some molecular linkers in the signaling pathways to the actin cytoskeleton have been detected. The range of downstream targets on the way from the actin cytoskeleton remains to be elucidated. Clearly, there is much more to learn how these diverse and closely interwoven pathways interact.

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