



Review

Signals fly when kinases meet Rho-of-plants (ROP) small G-proteins



Attila Fehér*, Dézi Bianka Lajkó

Institute of Plant Biology, Biological Research Centre, Hungarian Academy of Sciences, Temesvári krt. 62, H-6726 Szeged, Hungary

ARTICLE INFO

Article history:

Received 25 January 2015
 Received in revised form 11 May 2015
 Accepted 12 May 2015
 Available online 18 May 2015

Keywords:

Mitogen-activated protein kinase
 Protein phosphorylation
 ROP GTPase
 Guanine nucleotide exchange factor
 ROP-binding kinase
 Receptor-like kinase

ABSTRACT

Rho-type small GTP-binding plant proteins function as two-state molecular switches in cellular signalling. There is accumulating evidence that Rho-of-plants (ROP) signalling is positively controlled by plant receptor kinases, through the ROP guanine nucleotide exchange factor proteins. These signalling modules regulate cell polarity, cell shape, hormone responses, and pathogen defence, among other things. Other ROP-regulatory proteins might also be subjected to protein phosphorylation by cellular kinases (e.g., mitogen-activated protein kinases or calcium-dependent protein kinases), in order to integrate various cellular signalling pathways with ROP GTPase-dependent processes. In contrast to the role of kinases in upstream ROP regulation, much less is known about the potential link between ROP GTPases and downstream kinase signalling. In other eukaryotes, Rho-type G-protein-activated kinases are widespread and have a key role in many cellular processes. Recent data indicate the existence of structurally different ROP-activated kinases in plants, but their ROP-dependent biological functions still need to be validated. In addition to these direct interactions, ROPs may also indirectly control the activity of mitogen-activated protein kinases or calcium-dependent protein kinases. These kinases may therefore function as upstream as well as downstream kinases in ROP-mediated signalling pathways, such as the phosphatidylinositol monophosphate kinases involved in cell polarity establishment.

© 2015 Elsevier Ireland Ltd. All rights reserved.

Contents

1. Introduction.....	94
2. Kinases regulating ROP GTPase signalling.....	94
2.1. The CLAVATA1 receptor kinase complex.....	94
2.2. Pollen receptor kinases.....	95
2.3. FERONIA-type protein kinases.....	98
2.4. The transmembrane kinase receptor kinases.....	99
2.5. The PANGLOSS1 maize receptor-like kinase.....	100
2.6. The lysin motif domain receptor-like kinases.....	100
2.7. Further RopGEF-ROP signalling modules potentially linked to receptor kinases.....	101
2.8. Non-receptor protein kinases upstream of ROP GTPase signalling.....	101
3. Protein kinases regulated by ROP GTPase signalling.....	102
3.1. The ROP-activated receptor-like cytoplasmic kinases.....	103
3.2. The SNF1-related protein kinase type 2 kinase is indirectly regulated by Rops.....	104
3.3. ROP GTPases and the mitogen-activated protein kinase cascades.....	104
3.4. ROPs and lipid kinases.....	104
4. Conclusions and perspectives.....	104
Acknowledgements.....	105
References.....	105

* Corresponding author at: Institute of Plant Biology, Biological Research Centre, Hungarian Academy of Sciences, P.O. Box 521, H-6701 Szeged, Hungary.

Tel.: +36 62599701; fax: +36 62433434.

E-mail address: feher.attila@brc.mta.hu (A. Fehér).

1. Introduction

Rho-type small GTP-binding (or G-) proteins are among the key cellular signalling molecules in all eukaryotes (see, e.g., [1]). Their regulatory role is based on their capability to bind and hydrolyse GTP, and switch between two states: the active GTP- and the inactive GDP-bound conformations (Fig. 1). The GTP-bearing Rho G-proteins perform their regulatory function through a conformation-specific interaction with target (effector) proteins ([1]; Fig. 1). The power of G-proteins to alternate between active and inactive conformations allows these proteins to serve as ideal molecular switches for the transmission of discrete “ON–OFF” signals within the cells (Fig. 1). A number of regulatory steps control small G-proteins and fine-tune their signalling capacity (see, e.g., [2–4]; Fig. 1). G-protein activation is primarily achieved via the GDP-to-GTP exchange facilitated by guanine nucleotide exchange factors (GEFs). The inactivation of GTPases is the result of their intrinsic GTP-hydrolysing activity, stimulated by GTPase accelerator proteins (GAPs). Guanine nucleotide dissociation inhibitors (GDIs) regulate the membrane association and block the spontaneous activation of small GTPases. A further important biochemical feature of Rho proteins is their post-translational modification by lipids, determining their specific interaction with membrane microdomains.

Variations in the expression pattern, structure, and post-translational modification of Rho proteins influence their subcellular locations as well as their interactions with a number of upstream regulator and downstream effector molecules. These spatially and temporally regulated signalling relations allow these small GTPases to function as sophisticated modulators of a remarkably complex and diverse range of cellular processes. Rho G-proteins are primarily considered to have roles in the regulation of cytoskeletal functions, gene transcription, and the activity of plasma membrane NADPH oxidases [1–3].

Plants have a sole subfamily of Rho-type GTPases, called ROPs (Rho of plants), the members of which are structurally distinct from the proteins in the Rho, Rac, and Cdc42 subfamilies of other eukaryotes [2,3] (Table 1). The Rop subfamily is represented by 14 proteins in *Arabidopsis* and by seven in rice [5]. Some of the molecular mechanisms allowing ROPs to receive and transmit signals are conserved among yeasts, animals, and plants, whereas others are specific [3] (Table 1).

For example, the receptor tyrosine kinases and G-protein-coupled receptors that are upstream regulators of Rho-type GTPases in animals are most likely missing from plants [6,7]. However, plants do have a large number of receptor-like serine/threonine kinases [6]. The receptor-dependent activation of animal Rho-type G-proteins is mediated by guanine nucleotide exchange factors (GEFs), which are structurally unrelated in plants (Table 1). GEFs of non-plant Rho GTPases typically contain Dbl homology or DOCK180 catalytic domains, while most known RopGEFs have a specific plant ROP nucleotide exchanger (PRONE) domain with the same biochemical function [2]. The exception is a single DOCK180 domain-containing RopGEF, the SPIKE1 protein, described in *Arabidopsis* [8]. There is accumulating experimental evidence suggesting that receptor kinases regulate Rho GTPase signalling through GEFs in plants [9] as well as in animals [10], despite the fact that the participating proteins are distinct (Table 1).

It is not only the upstream ROP regulators that have specific features. ROPs share only a few downstream effectors with other eukaryotes (Table 1), such as the plasma membrane NADPH oxidase and certain actin nucleation complexes [3]. ROPs have several plant-specific effectors, including enzymes that have a role in cell wall synthesis, and plant-specific small scaffold proteins [2–4]. One of the most characteristic effector families of animal Rho-type GTPases—the Cdc42/Rac interactive binding motif-containing

(CRIB-containing) kinases (including Ste20 and related kinases in yeast, and the p21-activated kinases in animals; [11])—is missing from plants (Table 1). Our present knowledge on the link between ROPs and downstream kinase signalling is limited.

The aim of this review is to give an overview of the existing information about the insertion of ROP GTPases into upstream as well as downstream kinase signalling pathways in plants.

2. Kinases regulating ROP GTPase signalling

Signal perception through cell surface receptors is an important feature of all living organisms. The nature and abundance of various receptor configurations are highly divergent among the various taxa. A huge family of receptor serine/threonine kinases (usually referred to as receptor-like kinases), for example, characterizes land plants. The overall structure of these plant kinases (extracellular, transmembrane and cellular kinase domains) is very similar to that of the animal receptor tyrosine kinases, yet plant and animal receptor kinases have an independent evolutionary origin [6]. The abundance of plant receptor-like kinases is combined with the structural diversity underlying their functional divergence: they are involved in a variety of developmental, environmental and hormonal signalling pathways [12]. Due to the importance of this receptor family in plants, there have been considerable efforts to characterize its members, involving the identification of their ligands and downstream targets. These investigations have demonstrated that several plant receptor-like kinases affect the signalling activity of ROP G-proteins ([9]; see Sections 2.1–2.7).

In animal cells, receptor tyrosine kinase signalling to Rho proteins is a general signal transduction mechanism: more than half of the 58 known human receptor tyrosine kinases are implicated in Rho activation [10]. Receptor tyrosine kinases activate the Rho proteins indirectly, through the activation of RhoGEFs that facilitate the GDP-to-GTP exchange of Rho G-proteins [10]. Multiple receptor tyrosine kinases may activate the same RhoGEF-Rho signalling pathway, and the same receptor tyrosine kinase can activate multiple RhoGEFs/Rho proteins. Therefore, a complex combinatorial network of receptor tyrosine kinases, RhoGEFs and Rho proteins contributes to the specificity of the responses evoked by diverse signals in various tissue and cell types, each expressing a special subset of these proteins [10]. As discussed below in detail, recent findings indicate that similar signalling mechanisms have evolved in plants independently, since although plant receptor kinases, RopGEFs and ROPs are structurally different proteins from their functionally equivalent metazoan counterparts, they are also members of similar signalling modules. These presently recognized plant modules are summarized in Table 2, and are discussed in detail in Sections 2.1–2.7.

2.1. The CLAVATA1 receptor kinase complex

The first indication that ROP G-proteins and receptor-like kinases are interlinked came from the characterization of the *Arabidopsis* CLAVATA1 receptor-like kinase complex [13]. CLAVATA1 is a receptor kinase that regulates the size of the stem cell population in the *Arabidopsis* shoot meristem. CLAVATA1 is a member of two receptor complexes: one is 185 kD, the other is 450 kD [13]. Only the 450 kD complex, which was hypothesized to include the active receptor, contains a ROP G-protein as determined by co-immunoprecipitation experiments using CLAVATA1 and ROP antibodies. Due to the conserved structure of plant ROPs, the used antibody could not reveal which specific ROP GTPase was present in the complex. It was proposed that the active CLAVATA1 receptor signals, via the ROP protein, towards a mitogen-activated protein kinase (MAPK) cascade that controls WUSCHEL (a master regulator

Download English Version:

<https://daneshyari.com/en/article/2016966>

Download Persian Version:

<https://daneshyari.com/article/2016966>

[Daneshyari.com](https://daneshyari.com)