

# Connecting the dots: from nanodomains to physiological functions of REMORINs

Paul Gouguet, Julien Gronnier, Anthony Legrand, Artemis Perraki, Marie-Dominique Jolivet, Anne-Flore Deroubaix, Sylvie German-Retana, Marie Boudsocq, Birgit Habenstein, Sébastien Mongrand, et al.

# ▶ To cite this version:

Paul Gouguet, Julien Gronnier, Anthony Legrand, Artemis Perraki, Marie-Dominique Jolivet, et al.. Connecting the dots: from nanodomains to physiological functions of REMORINs. Plant Physiology, 2021, 185 (3), pp.632-649. 10.1093/plphys/kiaa063. hal-02996729

# HAL Id: hal-02996729 https://hal.science/hal-02996729v1

Submitted on 9 Nov 2020

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Connecting the dots: from nanodomains to physiological functions 

#### of REMORINS

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# **Abstract**

 REMORINs (REMs) are a plant-specific protein family, proposed regulators of membrane-associated molecular assemblies and well-established markers of plasma membrane nanodomains. REMs have been shown to play a diverse set of functions in plant interactions with pathogens and symbionts, responses to abiotic stresses, hormones signaling and cell-to-cell communication. In this review, we extensively highlight the roles and reported associations of REMs throughout the literature. We subsequently discuss the physiological functions of REMORINs, the mechanisms underlying their nanodomain-organization and their putative function as regulators of nanodomain-associated molecular assemblies. Furthermore, we discuss how REMORINs phosphorylation may regulate their functional versatility. Overall, through data-mining and comparative analysis of the literature, we suggest how to further study the molecular mechanisms underpinning the functions of REMs.

# **Advances Box**

- REMORINs are membrane-bound plant-specific proteins family involved in response to biotic (bacteria, viruses, fungi, oomycetes, mycorrhizae) and abiotic stresses (cold, mannitol, salt...), as well as developmental cues.
- REMORINs are strongly embedded in the inner-leaflet of the plasma membrane by an unconventional mechanism involving anionic lipids and sterols, and are proposed as nanodomain-organizing proteins.
- REMORINS are highly phosphorylated proteins containing intrinsically disordered regions, which likely play a role in scaffolding protein complexes.
- REMORINs regulate cell-to-cell communication through plasmodesmata.

# **Outstanding Questions Box**

- What are the molecular mechanisms underlying the formation of diverse and coexisting REMORIN nanodomains?
- How can REMORIN functional versatility be explained?
- What are the consequences of the phosphorylation(s) of REMORIN's intrinsically disordered regions in term of 3D structure, protein-protein interaction and nanodomain organization?
- How do REMORINs regulate cell-to-cell communication through plasmodesmata?

# **One-sentence summary**

This review collates and discusses all the available information on the plantspecific plasma membrane-bound family of REMORIN proteins involved in a plethora of cellular processes, likely as scaffolding factors.

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**DISCOVERY OF REMORINS** 

#### **REMORINS DISCOVERY**

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In this review on the plant-specific multigenic-family of REMORIN proteins (REMs), it is first important to remember how these proteins were discovered and came to be studied. REMs were first identified in tomato (Solanum lycopersicum) and potato (Solanum tuberosum) by Edward Farmer, Gregory Pearce and Clarence Ryan at the Institute of Biological Chemistry, Washington University, USA in 1989, in a will of identifying molecular actors involved in the perception of polygalacturonides by plant cells (Farmer et al., 1989). Polygalacturonides (PGA) are leaf pectic polysaccharides present in the plant cell wall which are released during wounding and pathogen attack. These cell wall compounds are molecules that the plant cell may perceive as an attack warning for a large range of pathogens (Voxeur and Höfte, 2016). It had been reported that PGA treatments were sufficient to induce the local and systemic release of proteinase inhibitors (Ryan and An, 1988). The plant secretes these proteinase inhibitors in order to counteract the potential proteases produced by the pathogens attacking the plant. Considering that these polysaccharides are not able to diffuse as fast as the systemic response is triggered, Farmer et al. investigated whether any signaling mechanism such as phosphorylation was activated at the plasma membrane (PM) of PGA-treated cells. Investigating phosphorylation events at the PM would enable the isolation of proteins able to perceive or relay the release of PGA in the apoplast. This would permit to subsequently explore the molecular agents involved in the systemic reaction triggered by wounding. It was in these *in vitro* phosphorylation assays on isolated tomato- and potato-PM that a clear band appeared on an electrophoresis gel at the molecular weight of 34 kilodaltons. This *phosphorylated protein* of <u>34</u> kilodaltons was therefore first called pp34 (Farmer et al., 1989). Consequently, pp34 was used as a marker for the plant-response to wounding, and by proxy, for the response to the most efficient PGA elicitor:  $\alpha$ -1,4-D-polygalacturonic acid (Farmer et al., 1991). By post-phosphorylation hydrolysis of pp34 and 2D electrophoresis, it was detected that the major phosphorylated residue in consequence to PGA treatment was Threonine with an 11-fold increase in phosphorylation (Farmer et al., 1991). The potato (Solanum tuberosum L.) pp34 was then purified after biochemical purification using a combination of phenol extraction and resolubilization after trichloroacetic acid (TCA) precipitation (Jacinto et al., 1993) and cloned by (Reymond et al., 1996). The sequence of pp34 turned out to be one of a hydrophilic protein

but unintuitively, still tightly bound to the PM. *Pp34* was then renamed REMORIN in reference to the work of J.L. Borges, "Book of Imaginary Beings" (*El libro de los seres imaginarios*, J.L. Borges, 1969), in which a remora or "suckerfish" is depicted as attaching itself to vessels and larger fish (Raffaele et al., 2007). The name REMORIN was therefore chosen by analogy to its binding to the PM whilst displaying an overall hydrophilic residue profile (Reymond et al., 1996). Concurrently to the experiments of Farmer et al., Alliote et al. isolated a similar protein in *Arabidopsis thaliana* termed <u>DNA-binding protein</u> (*dbp*). This gene would be later known as AtREM1.3 (At2g45820) and was first characterized as a DNA-binding protein due to its highly-hydrophilic nature permitting electrostatic interactions with DNA and its amino-acid composition similar to Histone 1 proteins (Alliotte et al., 1989).

Genome-wide analyses have shown that the REM family is specific to the land-plant lineage (Raffaele et al., 2007). REM proteins present a highly-conserved C-terminal domain and a divergent N-terminal domain, which has been the basis for their phylogenetic classification into 6 separate groups (Raffaele et al., 2007). For example, we count 19 OsREMs in rice Oryza sativa and 16 AtREMs in Arabidopsis thaliana. Note that during the writing of this review we found a 17<sup>th</sup> AtREM in the A. thaliana genome belonging to Group 2. We named it AtREM2.1 (At1g63295), see supplemental figure 1. Land plants have been evolving for 450-500 million years from an ancestral Charophycean algae (Delwiche and Cooper, 2015). BLAST analysis and keyword searches have identified no REM homologues in algal genomes (Raffaele et al., 2007), and a recent BLAST-analysis in Oestreococcus lucimarinus, Chlorella vulgaris, Volvox carteri, Chlamydomonas reinhardii, Ulva spp, and Micromonas pusilla has confirmed this statement (data not shown). Hence, the symbolism of the name REMORIN would come to be even more poignant, considering that the REM clade appears to have emerged in the first land plants (Raffaele et al., 2007). Naming this protein after a fish can be perceived as somewhat of an ironic twist if taken into account the putative role REMORIN proteins could have played in the adaptation of photosynthetic algae during the "plant land invasion" (Wellman, 2010).

Since their discovery in the late 1980's, REMs have been the subject of ever-increasing attention (Figure 1). Be they directly the subject of studies or found in different screens of "omics" approaches, REMs are consistently found in a large variety of academic inquiries,

providing grist to the mill to the idea that they could play a central role in plant development and adaptation. The first REMORIN protein identified in potato, which would be later named StREM1.3 for *Solanum tuberosum* REMORIN of Group 1 isoform 3. REMORIN's polyanion binding capacity, originally linked to binding cell wall compounds (Reymond et al., 1996) would be later mitigated by the discovery of REMORIN's presence as intrinsically inserted within the PM inner-leaflet (Raffaele et al., 2009). Nevertheless, the recent discovery of Group 1 REMs in a proteomic analysis of *A. thaliana* extracellular vesicles may potentially change our view of REMORIN's strictly-PM function (Rutter and Innes, 2017; Rutter and Innes, 2018).

In this review, we address the different characteristics that have been described for REMs as well as an overview of the physiological roles that REMs may participate in. We will discuss how REMs are anchored to the PM and cluster into PM-nanodomains, how they are phosphorylated and the subsequent role of these post-translational modifications. Finally, we will develop a number of perspectives on how REMs should be further studied in order to better understand the many physiological conditions involving REMs.

#### REMORINS LOCALIZE IN DIVERSE AND COEXISTING NANODOMAINS

REMORINs predominantly associate with the PM (Raffaele et al., 2009; Marín et al., 2012; Jarsch et al., 2014; Konrad et al., 2014; Perraki et al., 2014). Additionally to its PM localization, StREM1.3 has been used to immobilize ER-PM contact sites by using bimolecular fluorescence complementation (BiFC) (Tao et al. 2019). Moreover, isoforms from Group 1 and Group 6 REMs have been shown to be partially associated with the PD-PM compartment in rice and in Solanaceae (Raffaele et al., 2009; Fernandez-Calvino et al., 2011; Gui et al., 2014; Perraki et al., 2018). Nonetheless, translocation into the nucleus upon interaction with  $\alpha$ -importins (Marín et al., 2012) and re-localization to intracellular foci upon perception of an immunogenic epitope of bacterial flagellum (Albers et al., 2019) have been reported for Group 1 and Group 4 REMs, respectively.

Identification of Group 1 REMs in detergent-resistant membrane fractions (DRMs; a biochemical counterpart of membrane sub-compartmentalization) from tobacco first suggested a lateral organization of REMs into clusters at the PM (Mongrand et al., 2004).

REMs' co-purification with DRM appears to be dependent on the presence of phytosterols as it was reported to be absent of DRMs in the sterol methyl-transferase mutant *smt1* albeit still present in this fraction in the sterol glycosylation mutant *ugt80A2;B1* (Zauber et al., 2014). AtREM1.2 also appeared to have a sterol- and very-long-chain-fatty-acid -dependent patterning at the PM considering the "smoothing out" of its canonical patchy localization at the PM under fenpropimorph and metazachlor treatments (Grison et al., 2015).

Electron microscopy immuno-localization, stimulated-emission depletion (STED) microscopy and photoactivated localization microscopy (PALM) studies have all showed that Group 1 REMs were organized into nanodomains around about 70-90 nm in diameter in *Arabidopsis* and *Solanaceae* species (Raffaele et al., 2009; Demir and Horntrich, 2013; Gronnier et al., 2017). Members of other groups in *Arabidopsis* and *Medicago* are organized in PM domains that can be distinguished in density, size and shape (Jarsch et al., 2014). Interestingly, evolutionary distant REMs (belonging to distinct groups *e.g.* groups 1 and 6) localize in separate nanodomains hinting to that distinct REMs cluster into separate domains in order to play independent functions (Jarsch et al., 2014; Bücherl et al., 2017). It must also be noted that REMs of different groups are not found in the DRM-fractions of different plant tissues (Stanislas et al., 2009; Keinath et al., 2010; Srivastava et al., 2013; Takahashi et al., 2013), hinting to a diversity of REM-associated PM-domains and a dynamic-association of REMs within different domains.

### **Mechanisms of REMs Association to PM Nanodomains**

A number of works have been performed to understand how highly-hydrophilic REMs could be tightly anchored to the PM and the molecular interactions leading to the clustering of REMs into nanodomains. REMs are anchored to the PM inner-leaflet *via* the unconventional lipid-binding motif called REMORIN C-terminal Anchor (REM-CA) (Raffaele et al., 2009; Konrad et al., 2014; Perraki et al., 2014; Gronnier et al., 2017). In the past few years, several molecular determinants regulating REMs' nanodomain organization have emerged and need to be further studied to fully understand the diversity of REMs' clustering. There are at least four determinants: lipid-binding properties of REM-CA domain (that also can be S-acylated), lipid/lipid interactions, REM-REM oligomerization and REM-cytoskeleton interactions. Here we review the knowledge obtained to explain the molecular mechanisms at play.

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233 1. The unconventional membrane-anchoring REMORIN C-terminal Anchor domain (REM-CA) and S-acylation

REMs are synthesized in the cytosol as they contain no target-peptides or transmembrane domains (Raffaele et al., 2007). They attached to the PM independently of the conventional secretory pathway (Gronnier et al., 2017). In the case of StREM1.3, the last 28 amino acids (i.e. REM-CA) folds in the presence of specific lipids (Gronnier et al., 2017). This folding occurring during REM's interaction with the PM leads, or is concomitant, to REM-nanodomain formation. This is driven by protein-lipid interactions between the REM-CA and the PM's inner-leaflet lipids: negatively-charged phosphoinositides (PIPs), notably the Phosphatidylinositol-4-phosphate (PI4P), and sterols, notably sitosterol (Raffaele et al., 2009; Legrand et al., 2019), (Figure 2). REM-CA binds to PI4P with a yet unknown stoichiometry through its Lysine/Arginine residues by electrostatic interactions partially folds into an alpha helix in the presence of PI4P and sitosterol and also inserts itself into the hydrophobic core of the bilayer (Gronnier et al., 2017). Conceptually, with PIPs bearing mostly saturated acyl-chains (Furt et al., 2010), and their reported ability to cluster together to form nanodomains (Bilkova et al., 2017) together with the possibility for sitosterol to be recruited in the bilayer, as was shown in vitro for cholesterol (Engberg et al., 2016); REMs could be either targeted to pre-existing nanodomains or participate in the organization of their own lipid environments. Both the latter and former possibilities for REMs' association to PM-nanodomains still remain open questions. The presence of cysteine residues in the conserved REMORIN C domain of many REMs raised the possibility of membrane association due to S-acylation. AtREM1.2 was the first REM to be found to be S-acylated (Hemsley et al., 2013). SYMREM1 (MtREM2.2) as well as AtREM1.3, AtREM4.2, AtREM6.1 and AtREM6.3 have been described to be strictly PM localized thanks to their REM-CA moieties. AtREM1.2 and AtREM6.4 were also shown to need their REM-CA domains to localize at the PM, and all lost strict-PM localization when the REM-CA Cysteines residues were substituted by Alanine residues (Konrad et al., 2014). Yet for SYMREM1, the Cysteine substitution did not reduce its PM-localization and moreover did not change its segregation pattern in the PM, hinting to a more complex PM association

mechanism. Interestingly, AtREM6.4, which localizes to PM, has its localization altered to

intracellular vesicles when mutated at a C-terminal Cysteine residue (Konrad et al., 2014).

Altered localization when S-acylation is abolished via 2-bromopalmitate was also observed with the rice REM OsREM6.6 (Gui et al., 2015). This alteration of localization of S-acylationdeficient REM is reminiscent of the observation of the mutant NbREM1.1<sup>C206A</sup> and its relocalization to RFP-ATG8e-tagged vesicles (Fu et al., 2018). It is important to note that NbREM1.1<sup>C206A</sup> is no longer organized in nanodomains nor co-purifies with the DRM biochemical fraction (Fu et al., 2018). This highlights the importance of the REM-CA as a moiety strongly determinant of REM's general membrane affinity as well as REM's organization within these membranes. This idea is virtually illustrated in Fu et al. 2018 by the difference between NbREM1.1 and NbREM1.1<sup>C206A</sup> respective localization in both N. benthamiana epidermal cells and N. benthamiana protoplasts. Their localization varies from organized PM-domains to smooth PM-localization, respectively for wild-type NbREM1.1 and from smooth PM-localization to ER localization for the S-acylation mutant. These celldependent localization variations could be explained by different membrane and cell-wall compositions between these different cell types and also by the tissue-dependent native expression and localization patterns (Bariola et al., 2004; Jarsch et al., 2014). It must be noted that many other REMs do not have predicted S-acylation sites in their REMORIN\_C domain (Konrad et al., 2014; Gronnier et al., 2017).

# 2. REM Oligomerization

REM oligomerization is highly important for its stability and function. The first evidence of this phenomenon was reported in Bariola et al. (2004) where the REMORIN\_C coiled-coil domain of Group 1 REMs was first explicated as such and proposed to participate in the formation of REM multimers. Electronic microscopy and glutaraldehyde crosslinking assays evidenced REM multimerization *via* the C-terminal region of two Group 1 REMs *i.e.* StREM1.3 and SIREM1.2 (Bariola et al., 2004). This multimerization has been discussed in a few papers with yet no *in vivo* proof of the order of oligomerization (Jaillais and Ott, 2020). Bariola et al. (2004) argue *via* analytical ultracentrifugation of recombinant proteins and cross-linking experiments on isolated PM that Group 1 REMs associate into dimers, tetramers or higher-order oligomeric structures *via* their coiled-coil domains. Alternatively, Perraki et al. (2012) developed the hypothesis that StREM1.3 would trimerize either before

or after the anchoring event at the PM. This hypothesis was upheld by gel filtration assays with the *E. coli* purified 6His-tagged StREM1.3 protein.

In our current view, StREM1.3 is homo-trimeric in solution and in certain assembled configurations (Bariola et al., 2004; Martinez et al., 2018), bundling three REM-CA domains together. This trimeric hypothesis was further developed in Martinez et al. (2018) upon in silico modelling confirmed by Solid-State NMR in conjunction with cryo-Electron Microscopy (cryo-EM) and in vivo observations of mutations in the coiled-coil domain that impairs PMassociation (Figure 2). These in vivo observations seem to corroborate the hypothesis that in a minimal state, the trimeric form is necessary for the anchoring to the PM. Cryo-EM further revealed a possible lateral association of the trimeric REMs in the presence of an N-terminal 6His-tag (Martinez et al., 2018), yet the presence of a 6His-tag may also alter the oligomeric behavior of proteins (Amor-Mahjoub et al., 2006). This casts a doubt on the trimer observed by gel filtration. In any case, the existence in vivo of homo-oligomers and higher-order oligomers has not been invalidated by the latest data. Because of steric hindrance between the oligomers and the lipid headgroups, as well as considering protein-lipid interactions, the overall REM orientation is likely rather perpendicular to the PM, placing the REM-CA domains of the oligomeric REMs symmetrically on the lipid headgroups (Figure 2). Formation of higher-order oligomers, i.e. oligomers of trimers, as a mean to drive nanoclustering cannot be excluded but has yet to be tested. Interactions between the REM trimers are likely to further stabilize nanodomain clustering.

Group 1 AtREMs have been found to form oligomers in a large-scale study of PM protein oligomerization in leaves (McBride et al. 2017). AtREM1.2, AtREM1.3 and AtREM1.4 were predicted to form oligomeric complexes according to their ratio of the calculated mass to the apparent mass (R<sub>app</sub>) score which calculates a ratio between the predicted molecular mass of the monomer and the measured molecular mass of the complex in which the protein is found. AtREM1.2, AtREM1.3 and AtREM1.4 were found in different complexes to have R<sub>app</sub> scores ranging on average from 35 to 60 for AtREM1.2, 25 for AtREM1.3 and 30 to 95 for AtREM1.4 (McBride et al. 2017). This data may suggest that in addition to being homo-oligomerized, Group 1 REMs are also forming multi-protein complexes. This idea has already been suggested in the literature, notably in Lefebvre et al. (2010) where REMs are

compared to caveolins considering the common properties they share: small, oligomeric, lipid raft-associated scaffold proteins that can form filamentous structures.

#### 3. REM Association with the Cytoskeleton

In the seminal work of Jarsch et al. (2014), the subcellular localization of all Arabidopsis REMs was studied, and certain members displayed characteristic patterns at the PM. Observed filamentous exclusion zones (Jarsch et al., 2014) at the surface of the PM have led to think that REMs could be associated in some way with the cortical cytoskeleton. A localization dependent on microtubule polymerization has been reported for AtREM6.6 (Jarsch et al., 2014) as well as for AtREM1.2 (Szymanski et al., 2015) using the microtubule depolymerizing drug oryzalin. Oryzalin treatment substantially mislocalized these REMs, that were originally at the PM in domains (AtREM1.2; Szymanski et al., 2015) or forming strands in the cytosol (AtREM6.6; Jarsch et al., 2014). An association with the actin cytoskeleton may also be hypothesized considering the localization of the N-terminal regions of AtREM4.2 and AtREM6.5 (Jarsch et al., 2014).

This interplay between the cortical cytoskeleton and PM-nanodomains fits with the "fences and pickets" paradigm (Kusumi et al., 2012), where REMs could play a role as a putative scaffold protein. This interplay with actin has been further demonstrated for other REMs such as SYMREM1 (also termed MtREM2.2), a crucial actor involved in bacterial symbiosis establishment in Medicago truncatula. MtREM2.2's association to PMnanodomains has been shown to be destabilized by the actin depolymerizing drug, latrunculin B, yet not by the microtubule depolymerizing drug, oryzalin. MtREM2.2's presence at the PM was also shown to be essential for the establishment of FLOT4-LYK3 domains that are dependent on the contact between FLOT4 and the actin cytoskeleton (Liang et al., 2018). The rice Group 6 REM, OsREM6.6 or GSD1, has also been shown to interact with the actin cytoskeleton. It was shown to bind OsACT1 in planta as long as its REM-CA region was S-acylated (Gui et al., 2015). Treatment with cytochalasin D (a potent inhibitor of actin polymerization) completely disrupted the punctate localization pattern of AtREM1.2 and AtREM1.3 to a more uniform distribution with smaller punctate patterns of lower intensity (Szymanski et al., 2015). Additionally, AtREM1.2 was shown to associate with the actin cytoskeleton under viral infection (Cheng et al., 2020). This data reveals the strong relationship between REMs' anchoring to the PM and the actin cytoskeleton in order to ensure their function.

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#### THE BIOLOGICAL FUNCTIONS OF REMORINS

#### Plant-Microbe Interactions

Numerous studies have reported the implication of REMs in plant interactions with microorganisms such as bacteria, viruses or filamentous pathogens/symbionts (*i.e.* fungi and oomycetes).

#### 1. Bacteria:

The involvement of REMs in plant-bacteria interactions has mainly been studied in the context of Group 2 REMs implicated in the establishment of bacterial symbiosis in legumes. Yet several studies have also reported the involvement of Group 1 REMs in responses to pathogenic bacteria.

#### Group 2 REMs & Bacterial Symbiosis

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The particular Group 2 REMs, merely constituted of a REMORIN C DOMAIN (Raffaele et al., 2007), have been characterized by their role in the establishment of infection threads (IT) during the symbiosis of M. truncatula and Lotus japonicus with Rhizobiaceae family bacteria by participating in the formation of a root nodule (Lefebvre et al., 2010; Tóth et al., 2012). SYMREM1 (MtREM2.2) in M. truncatula has been shown to be specifically expressed in roots and nodules with an expression strongly induced by Nod factors treatment (Lefebvre et al. 2010), which are lipo-chitooligosaccharides produced by symbiotic bacteria or fungi in order to initiate symbiosis (for review: Oldroyd 2013). Furthermore, MtREM2.2 knock-down lines were shown to strongly reduce nodule establishment and growth (Lefebvre et al. 2010). Analogously overexpression of Group 2 REM LjSYMREM1 significantly increased the number of nodules per root in L. japonicus, establishing these orthologs as key players for symbiosis in legumes (Tóth et al., 2012). In this context, MtREM2.2 has been further characterized at the molecular level. It has been described as a scaffold protein due to its interaction with three receptor-like kinases (RLKs) essential for nodule establishment and maintenance i.e. NFP, DMI2 and LYK3 (Lefebvre et al., 2010). This interaction has recently been further associated to the effective role of these membrane-bound receptors and MtREM2.2 along with FLOT4 (FLOTILLIN 4) in the initiation of IT (Liang et al., 2018). MtREM2.2 is believed to stabilize the interactions between FLOT4 and both NFP and LYK3 which would prevent the RLKs' endocytosis and ensure nodulation-promoting signaling (Liang et al., 2018; see Figure 3A).

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#### Group 1 REMs & Bacterial Pathogenicity

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Considering the presence of Group 1 REMs within PM-nanodomains (Raffaele et al., 2009) that are known to host many proteins involved in plant innate immunity such as RLKs and other innate immunity-associated proteins (Morel et al., 2006; Stanislas et al., 2009; Keinath et al., 2010), their involvement in these processes was long suspected. Under treatment by the ubiquitous bacterial elicitor flagellin (flg22), AtREM1.3 was found to be differentially phosphorylated up to 3-fold more on its Threonine 58 and approximately 1.5-fold on its Serine 14 (Benschop et al., 2007). It must be noted that this large-scale phosphoproteomics screen did detect other A. thaliana REMs such as AtREM1.2, AtREM5.1, AtREM6.1, AtREM6.2 and AtREM6.4 but they were not reproducibly differentially phosphorylated under flg22 or xylanase treatments (Benschop et al., 2007). It is interesting to find a differential phosphorylation status between AtREM1.3 and AtREM1.2 considering that they colocalize in vivo (Jarsch et al., 2014). However, AtREM1.2 possesses Alanines at the two phosphosites detected to be differentially phosphorylated under flg22 treatment (i.e. Ser14 and Thr58) (Benschop et al., 2007; Raffaele et al., 2007). This suggests that there may be (a) specific kinase(s) triggered under flg22 treatment that could recognize these sites. Moreover, a thread of evidence leads to the implication of AtREM1.2 and AtREM1.3 in the cell's response to bacterial infection. AtREM1.2 has been shown to be significantly up regulated at the protein level in plants over-expressing the Pseudomonas syringae effector gene AvrRPM1 (Widjaja et al., 2009). Different AtREM1.2 post-transnationally modified peptides (putative phospho-peptides) were recovered in this screen for low-abundant proteins involved in plant defense, confirming the implication of AtREM1.2 in the general response to bacterial infection (Widjaja et al., 2009), see supplementary table 1.

The AtREM1.2 has been shown to interact with RPM1 (RESISTANCE TO PSEUDOMONAS SYRINGAE PV. MACULICOLA 1)- INTERACTING PROTEIN 4 (RIN4), an interacting partner of RPM1 involved in bacterial disease resistance known as a negative-regulator of Pathogen-associated Molecular Pattern (PAMP)-Triggered Immunity (PTI), more precisely PTI linked to

Pseudomonas syringae (Mackey et al., 2002; Liu et al., 2009a; Lee et al., 2015). In response to bacterial attack and notably to the presence of the bacterial effector AvrRpm1 or AvrB, RIN4 is known to be hyper-phosphorylated, thereby leading to RPM1-mediated resistance (Mackey et al., 2002). RIN4 is also known to contain a protein cleavage site that can be targeted by the *P. syringae* effector AvrRpt2 (as well as AtREM6.1; *in silico* prediction (Chisholm et al., 2005) and induce RPS2-mediated resistance (Mackey et al., 2002). Induced-phosphorylation of AtREM1.2 by the expression of avirulence pathogen genes is dependent of RPM1 nucleotide binding site leucine rich repeat (NB–LRR) immune receptor (Widjaja et al., 2009). Overall these data may suggest that AtREM1.2 lies at the crossroads of Effector-Triggered Immunity (ETI) and PTI.

Additionally, AtREM1.2 and AtREM1.3 along with RIN4 have been identified as interactors of the *P. syringae* effector HopF2b<sup>PtODC3000</sup> via the proximity-dependent biotin identification (BioID) technique that uses the *E. coli* biotin ligase BirA\* to biotinylate potential interacting proteins that come in proximity to BirA\*-fused bait protein, here HopF2b<sup>PtODC3000</sup> (Khan et al., 2018). This triggers the questions whether bacterial effector proteins may target REMs to suppress their function in immunity or if REMs are involved in perceiving bacterial effector proteins. The implication of REMs in bacterial immunity remains to be deciphered further.

In *Solanaceae*, REMs have scarcely been reported as being involved in bacterial interactions except for the potato REM StREMa4 (StREM1.4) that has been described as differentially regulated under *Ralstonia solanacearum* infection (Kong et al., 2016). StREM1.4's expression has been shown to be upregulated at 6- and 72-hours post-infection and mainly expressed in the vascular bundle of leaves and the phloem of stems (Kong et al., 2016). This data suggests that StREM1.4 may be involved in the regulation of innate immunity/cell-to-cell communication in the latter tissues considering its high-homology to StREM1.3 and the fact that *R. solanacearum* is a bacterial pathogen that colonizes the vascular tissue of *S. tuberosum* plants.

# 2. Viruses

The first REM to be shown as implicated in the context of viral infection has been StREM1.3. It has been demonstrated that its overexpression, leads to the limiting of the cell-to-cell movement of *Potato Virus X* (PVX) (Raffaele et al., 2009) and, had a general effect on the gating of PD even in the presence of viral movement proteins such as 30K from the

Tobacco Mosaic Virus (TMV) or Hc-Pro from the Potato Virus Y (PVY) (Perraki et al., 2014). In addition to limiting PVX cell-to-cell movement, StREM1.3 has also recently been shown to limit TMV cell-to-cell propagation (Perraki et al., 2018). Over-expression of StREM1.3 was shown not to impair the silencing suppressor activity of the PVX-encoded TRIPLE-GENE BLOCK protein 1 (TGBp1) (Perraki et al., 2012), but rather to induce the increase in callose accumulation at PD pit-fields (Perraki et al., 2018). Furthermore, StREM1.3's capacity in hindering PVX cell-to-cell movement has been shown to be abolished by altering the electrostatic properties of the REM-CA, thereby modifying its localization pattern at the PM (Gronnier et al., 2017). Yet, StREM1.3 was shown to physically interact with the PVX movement protein TGBp1 with or without an impaired REM-CA domain (Perraki et al., 2012). Solanaceae Group 1 REMs have also been studied in the context of Tenuivirus infection. N. benthamiana NbREM1.1 and NbREM1.2 were shown to be degraded during Rice Stripe Virus (RSV) infection in consequence to the interference of the RSV-encoded protein, NSvc4, with the S-acylation of these Group 1 REMs' REM-CA. The degradation of NbREM1.1 and NbREM1.2 via the autophagy pathway led to RSV circumventing NbREM1-associated resistance (Fu et al., 2018). In contrast, a recent study has underlined the effect of the tobacco REM NtREM1.2 on the cell-to-cell movement of a Tobamovirus, the Tomato Mosaic Virus (ToMV) (Sasaki et al., 2018). ToMV infection and the overexpression of ToMV movement proteins separately affected NtREM1.2's localization by inducing its aggregation at the PM. Dissimilarly to StREM1.3, which is known to localize in a patchy pattern at the PM and is present in PM-nanodomains, NtREM1.3 localized in a uniform fashion throughout the PM regardless of N-terminal or C-terminal fusion to fluorescent tags. Considering the high sequence conservation of the C-terminal region, this suggested that the N-terminal region was involved in NtREM1.2's characteristic localization. Interestingly, NtREM1.2 was shown to interact and colocalize with ToMV's 30-kDa movement protein at PD using BiFC and aniline blue staining. Agrobacterium-mediated transient expression of NtREM1.2 was also shown to slightly increase ToMV infection foci size (Sasaki et al., 2018). Moreover, in ToMV infected cells, NtREM1.2 aggregates occur close to tubular ER structures and are associated with ToMV's 30-kDa movement protein bodies that appeared to be linked to the Endoplasmic Reticulum-Actin network (Sasaki et al., 2018). Finally, A. thaliana AtREM1.2 has been shown to play a role in Turnip Mosaic Virus (TuMV) cell-to-cell movement by competing with the TuMV protein VPg, in the actin-dependent regulation of PD aperture (Cheng et al., 2020).

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Group 4 REMs have been reported as positive regulators of viral infection. AtREM4.1 and AtREM4.2 were shown to be susceptibility factors during *Beet Curly Top Virus* and *Beet Severe curly Top Virus* infection. This was shown using single- and double- knock-out and overexpressing lines for AtREM4.1 and AtREM4.2. This effect of Group 4 REMs on geminiviral infection could be linked to SnRK1, an important positive regulator of plant stress involved in antiviral defense, which could phosphorylate AtREM4.1 *in vitro* (Son et al., 2014).

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# 3. Fungi and Oomycetes

REMs have been reported to be directly implicated in interactions with filamentous pathogens/symbionts.

# Filamentous pathogens

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StREM1.3 has long been established as a marker of Phytophthora infestans haustoria (Lu et al., 2012; Bozkurt et al., 2014). The extrahaustorial membrane (EHM) is a host PM-derived membrane formed by the protrusions of the oomycete (haustoria) within the plant cell known to occur in the early stages of the infection and are thought to be a hub for nutrient intake as well as effector delivery by the pathogen (Dagdas et al., 2016). StREM1.3 has been observed to label haustoria approximately 50 % of the time and specifically label non-callosic haustoria (Bozkurt et al., 2014). Moreover, the overexpression of StREM1.3 in N. benthamiana and tomato increased susceptibility to P. infestans infection (Bozkurt et al., 2014). Nevertheless, the true role of StREM1.3 during *P. infestans* has yet to be precisely determined. Interestingly, recent studies showed the specific recruitment of phosphoinositides (PIPs) to the plant-pathogen interfacial membrane during fungal infection (Qin et al., 2020). Different PIPs were found enriched at EHM. Researchers demonstrated that among the two PM phosphoinositides in Arabidopsis, Phosphatidylinositol 4,5bisphosphate (PI(4,5)P<sub>2</sub>) was dynamically up-regulated at powdery mildew infection sites and recruited to the EHM, whereas PI4P is absent in the EHM. Furthermore, the depletion of PI(4,5)P<sub>2</sub> in the pip5k1 pip5k2 mutant lines inhibited fungal pathogen development and caused disease resistance, independent of cell death-associated defenses, involving impaired host susceptibility. The fact that REMs both bind to PIPs and are involved in immune responses to fungi prompted to examine in detail the link between these two observations.

The first report of the implication of REMs in plant-fungal interactions was a maize Group 6 REM ZmREM6.3 that was found in a QTL (Quantitative Trait Loci) analysis for resistance to northern leaf blight caused by the fungal pathogen *Setosphaeria turcica* (Jamann et al., 2016). The importance of Remorins for the resistance of maize to fungal pathogens has also been highlighted by the importance of ZmREM1.3 in the resistance to *Puccinia polyspora* (Wang et al., 2019). AtREM1.3 was also found to interact with ergosterol, a fungal metabolite toxic for plants (Khoza et al., 2019). Cucumber (*Curcumis sativus*) CsREMs that presumably (*i.e.* closest ortholog annotations found using NCBI *BLASTp*) belong to Group 4 (Sequence ID: XP\_004134586.1) and Group 1 (Sequence ID: XP\_004133871.1; closest *A. thaliana* ortholog: AtREM1.2) have been found to be present in a QTL genomic segment termed *Pm5.1* and to be differentially expressed upon powdery mildew (*Podosphaera fusca*) infection (Xu et al., 2017). These REMs are proposed to participate in the resistance to powdery mildew conferred by the *Pm5.1* segment (Xu et al., 2017).

A recent study showed that overexpression of tomato (*Solanum lycopersicum*) SIREM1 increased susceptibility to the necrotrophic fungus *Botrytis cinerea* (Cai et al., 2020). Heterologous expression of SIREM1 increased ROS accumulation and triggered other cell-death regulators, suggesting a positive role of SIREM1 in plant cell-death and providing clues for understanding the PCD molecular regulatory networks in plants.

Along with herbivores, pathogenic insects and bacteria, filamentous pathogens are known for wounding plant tissue, yet out of all the latter-named pathogens, they are particularly known for the diverse cell wall-degrading enzymes they are able to synthesize and secrete (for review Kubicek et al., 2014). Therefore, the initial discovery of Group 1 REMs as being phosphorylated subsequently to the presence of cell wall degradation products (e.g. PGA; Reymond et al., 1995) hints to the association of Group 1 REMs to the response to fungal attack. An emerging field of research has been concentrating on the vesicular exchanges that may occur during plant pathogen interactions. These extracellular vesicles (EVs) are produced by the host and the pathogen and may contain a number of defense compounds such as defense proteins, metabolites or interfering-RNAs involved in post-transcriptional gene silencing (for review, Rutter and Innes, 2018; Rybak and Robatzek, 2019; Cui et al., 2020). Congruently, EVs have been reported to accumulate in large numbers at the pathogenic fungi penetration sites produced by appressoria and haustoria (Meyer et

al., 2009; Micali et al., 2011). The presence of AtREM1.2 and AtREM1.3 in A. thaliana extracellular vesicles alongside stress related proteins and compounds may well be a telltale sign of Group 1 REMs' direct involvement in plant defense (Rutter and Innes, 2017). Coming back to the recorded PGA-binding capacity of Group 1 REMs (Reymond et al., 1996), it could have initially seemed unlikely that their presence in EVs is linked to this phenomenon considering that AtREMs were not found to be phosphorylated under PGA-treatment, unlike REMs from other species (Reymond et al., 1996). Nonetheless, more recent phosphoproteomes of oligogalacturonide (OGA)-treated plants have been established and have found AtREM1.3 and AtREM1.2 to be phosphorylated under OGA (degree of polymerization = 9-15) treatment (Kohorn et al., 2016; Mattei et al., 2016). One of the canonical markers of extracellular vesicles, PENETRATION3 (PEN3) was also found to be phosphorylated under OGA treatment (Kohorn et al., 2016; Mattei et al., 2016). PEN3 is an ATP Binding Cassette ABC transporter family protein and is thought to participate in the transport of defense compounds along with other EV-resident proteins such as GTR1 (GLUCOSINOLATE TRANSPORTER1; At3g47960) and EPITHIOSPECIFIC MODIFIER1 (ESM1; At3g14210) involved in glucosinolate biosynthesis and transport (Rutter & Innes 2017). Moreover, RIN4 has also been found in the EV proteome along with EARLY-RESPONSIVE TO DEHYDRATION4 (ERD4; At1g30360) which are known to interact with AtREM1.2 (Liu et al., 2009b; Khan et al., 2018). This data may open new perspectives in understanding Group 1 REMs' role in link to wounding response.

A recent protein- and metabolite-profiling of tomato and lettuce infected with *Verticillium dahlia*, a soilborne fungal pathogen, showed that REMs were expressed in the incompatible interaction together with lignin biosynthesis, phenylpropanoid, and carbohydrate methylation pathways. Authors proposed that this response allows the strengthening of plant cell walls, likely critical to confer resistance to *V. dahliae* (Hu et al., 2019).

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# Filamentous symbionts

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A couple of papers have reported the implication of REMs in the establishment of mycorrhizal symbiosis. The oak (*Quercus robur*) Group 4 REM QrREM4.1 (Accession number: Qrob P0167880.2) was transcriptionally detected in roots undergoing ectomycorrhizal

symbiosis with *Piloderma croceum* (Tarkka et al., 2013). An ortholog of Group 1 REMs (Accession number: AFK42693.1) has been reported to be transcriptionally up-regulated in *L. japonicus* roots 3-weeks post-inoculation with the ectomycorrhizal symbiotic fungi *Glomus intraradices* (Kistner et al., 2005).

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# **Hormone Signaling & Abiotic Stress**

Throughout the relatively extensive literature that links the expression of REMs to hormone signaling and/or abiotic stress, several patterns may be found. Considering the overlapping nature of these types of events, we will proceed by grouping REMs by phylum in order to describe the relevant data present in the literature.

# 1. Group 1 REMs

Group 1 REMs have been found to be transcriptionally up regulated in a large variety of abiotic stress conditions. AtREM1.3 was initially found to be induced under water deficit conditions (Reymond et al., 2000; Bray, 2002) as well as under cold, mannitol and salt stress (Kreps et al., 2002). These types of stress are reminiscent of abscisic acid (ABA)-signaling conditions. AtREM1.3 transcription has also been shown to be induced by auxin treatment in the shoot apex, particularly in regions undergoing cell division (Alliotte et al., 1989). This same isoform had also been found to interact with ARR4, an Arabidopsis response-regulator induced by cytokinin treatment (Yamada et al., 1998). The arr4 mutant displays an elongated petiole phenotype (Verma et al., 2015). Group 1 REM isoforms from crops have evidenced to be involved in hormonal signaling linked to development and stress responses. The tomato SIREM1.2 has recently been shown to be involved in fruit ripening by interacting with the ethylene biosynthesis proteins SAM1, ACS2 and ACO1. The overexpression was also shown to up-regulate key genes involved in ethylene, lycopene biosynthesis and ripening regulators (ACS2, ACS4, ACO1, ACO3, RIN, NOR, CNR, TAGL1, SIDML2, SIMSI1) resulting in an effective increase in the ethylene and lycopene content of fruit (Cai et al., 2018). This same tomato REM isoform was found to be consequently transcriptionally upregulated (more than 9-fold) in tomato plants overexpressing CaPIF1, a pepper zinc-finger transcription factor known to be involved in resistance to bacterial infections (Oh et al., 2005; Seong et al., 2007). The resulting CaPIF1 overexpressing lines were characterized by an enhanced resistance to cold stress (Seong et al., 2007).

The functional characterization of a mulberry (*Morus indica*) Group 1 isoform MiREM1 evidenced its transcriptional upregulation under a number of abiotic stresses and hormone treatments *e.g.* air drying, ABA, SA, BR treatments and mannitol and salt stress in the aerial parts of the plant. Heterologous overexpression of MiREM1 in *A. thaliana* conferred resistance to salt stress and drought in the extent that the overexpressing lines better recovered from drought stress and maintained a higher fresh weight and root length than the wild-type lines during salt stress (Checker and Khurana, 2013).

The potato StREM1.4 (or StREMa4) was found to be transcriptionally up regulated under MeJA treatment up to 7-fold at 3 days post-treatment. On the other hand, ABA and SA increased StREM1.4 transcription roughly 20-fold at 4 days and 4-fold at 5 days, respectively. Interestingly, *in situ* hybridization of StREM1.4 transcripts revealed its presence in the vascular bundles of leaves and phloem of stems (Kong et al., 2016). In strong correlation with this study, AtREM1.2's lipid-dependent presence and organization at the PM was shown to be a major determinant of SA-dependent closure of PD (Huang et al., 2019). Likewise, the rice Group 1 isoform OsREM1.5 was found to be more than 2-fold up-regulated by ABA and BR treatments (Lin et al., 2003). The up-regulation of Group 1 REM isoforms seems to be a common feature in the aerial tissues under a variety of hormone treatments and abiotic stresses, yet a study performed on barley aleurone (*Hordeum vulgare L. cv Himalaya*) showed downregulation of the Group 1 REM HvREM1 upon ABA and GA treatments (Chen and An, 2006).

# 2. Group 4 REMs

Group 4 REMs also appear to be induced by abiotic stresses and hormone treatments in different plant species. AtREM4.1 and AtREM4.2 are transcriptionally upregulated by drought, osmotic, salt stress and ABA treatment (Reymond et al., 2000; Bray 2002; Son et al., 2014). In soy (*Glycine max*), GmREM4 transcript abundance was overall shown to increase in drought conditions over a 20 hour-period and even more under "severe drought" conditions. In addition, GmREM4 always followed diurnal oscillations with minimal expression in the middle of the light period (Marcolino-Gomes et al., 2014). More than just showing a transcriptional increase of Group 4 REMs during drought stress, this study brings to light a circadian regulation of REMs, likely to be crucial for their function.

The rice (*Oryza* sativa) OsREM4.1 was shown to be up regulated by ABA treatment *via* the bZIP transcription factor OsZIP23, which can bind the OsREM4.1 promoter. OsREM4.1 overexpression inhibited BR signaling by inhibiting OsSERK1 and OsBRI1 complex formation. This REM effect is undermined by the phosphorylation of REM. Under high ABA concentrations, OsREM4.1 is up regulated by OsZIP23 and inhibits the formation of the OsSERK1/OsBRI1 complex. Under high BR concentrations, BR stabilizes the OsSERK1/OsBRI1 complex, which activates the phosphorylation of OsREM4.1 by OsBRI1, thereby reducing OsREM4.1's affinity for OsSERK1 and enabling the BR signaling cascade. This system maintains a dynamic equilibrium between ABA and BR signaling (Gui et al., 2016a), see Figure 3B.

Overexpressing in rice a C-repeat binding factor (CBF)/dehydration-responsive element binding protein (DREB) of the Antarctic plant *Deschampsia antartica*, DaCBF7, enhanced cold recovery and induced the strong up regulation of OsREM4.1 (5- to 10-fold higher than in WT lines regardless of stress) (Byun et al., 2015). In maize (*Zea mays* L.), Group 4 REM ZmREM4.1 transcripts were found in several tissues: Kranz mesophyll, bundle sheath, vascular parenchyma, companion cells and sieve elements, with a specific accumulation between the Kranz mesophyll and the bundle sheath. REM was shown to be transcriptionally repressed in a maize cold-sensitive line after 28h (Bilska-Kos et al., 2016).

# 3. Group 6 REMs

The Group 6 REM SiREM6 (*Setaria italica*, fox-tail millet) has been found to be transcriptionally up regulated under salt (NaCl 150mM), cold (4°C), ABA (100μM) and osmotic (PEG 20% v/v) stress up to 12h post-stress. Yet this up regulation was weakly observed under drought stress and SiREM6 overexpression did not impact drought tolerance (under 300mM mannitol). SiREM6 overexpression in *A. thaliana* increased germination rate and seedling biomass as well as seedling survival under salt stress. These characteristics were linked to an increase in proline content and a reduction in electrolyte leakage. Additionally, overexpression of SiREM6 in *A. thaliana* enhanced sensitivity to ABA treatment (Yue et al., 2014). In rice (*Oryza* sativa), OsREM6.5 was also found to be highly upregulated during drought stress (7.8-fold) and ABA treatment (9.5-fold) (Wu et al., 2006).

In *Populus euphratica*, a salt-resistant poplar, PeREM6.5 was induced by NaCl stress. Interestingly, PeREM6.5 recombinant protein significantly increased the H<sup>+</sup>-ATPase hydrolytic activity and proton transport activity in *P. euphratica* PM vesicles. Yeast two-hybrid assays showed that PeREM6.5 interacted with RPM1-interacting protein 4 (PeRIN4) and PeREM6.5 induced an increase in H<sup>+</sup>-ATPase activity that was moreover enhanced by PeRIN4 recombinant protein. Finally, overexpression of PeREM6.5 in *A. thaliana* improved salt tolerance. PeREM6.5, by regulating H<sup>+</sup>-ATPase activity in the PM, may therefore enhance the plant capacity to maintain ionic homeostasis under salinity (Zhang et al., 2020).

More generally, a recent genome-wide analysis of the wheat genome *Triticum aestivum* revealed that 12 members of the TaREM family of different groups were regulated during cold acclimation in wheat in four different tissues (roots, crowns, stems, and leaves), with the highest expression in roots (Badawi et al., 2019). This study provides valuable resources for functional analysis aimed at understanding the role of TaREMs in stress adaptation.

# **Cell-to-Cell Communication**

Throughout the different contexts that implicate the presence of REMs in the plants' adaptation to the various aforementioned stimuli, one constant seems to stand out, which may well explain the fact that REMs are so ubiquitously present in such diverse contexts: cell-to-cell communication.

The first direct evidence of the implication of REMs in cell-to-cell communication was revealed by the ability of StREM1.3 to hinder PVX cell-to-cell movement as well as GFP diffusion in non-virally-infected plants in *N. benthamiana* leaf epidermal cells (Perraki et al., 2012; Perraki et al., 2014). This capacity was shown to be dependent of the REMORIN\_C domain, shown to be responsible for its anchoring to the cytosolic leaflet of the PM (Perraki et al., 2012; Gronnier et al., 2017). Conversely, Group 4 REMs have been evidenced to potentially have an opposite effect on cell-to-cell connectivity. OsREM4.1 transcripts were found to be localized in situ near PD linking cells from the Kranz mesophyll and the bundle sheath (Bilska-Kos et al., 2016). This interface is a crucial zone for the systemic diffusion of macromolecules necessary for plant development and for the plant-wide adaptation to

various biotic or abiotic stimuli. These observations could explain the data demonstrating that AtREM4.1/4.2 positively regulate BSCTV and BCTV systemic infection in *A. thaliana* (Son et al. 2014). This tissue-specific expression, REM group specificity and evidence of REMs' involvement in cell-to-cell communication seem to be the key to understanding this characteristic of REM function. Moreover, REM transcript and protein levels were shown to increase in mature, ageing and senescing tissues, as well as in source parts of tobacco leaves, where a majority of mature- and branched-PD are present (Raffaele et al., 2009). These results suggest that tobacco Group 1 REMs predominantly associate with mature-branched-PD.

The Group 6 REM OsREM6.6 was shown to be a strong regulator of PD permeability in rice via the characterization of a tissue-specific expression mutant line. The mutant termed GSD-1 (for grain setting defect 1) was shown to have an altered and ubiquitous expression of OsREM6.6, which is natively only expressed in phloem companion cells, thereby inducing an accumulation of starch and free-sugars in the leaf blades and consequently a reduction of starch accumulation in grains (Gui et al., 2014).

The only occurrence in the literature of Group 5 REMs in regard to development and indirectly cell-to-cell communication, has been the identification of Long Panicle 1 (LP1 or OSREM5.3) displaying higher expression (6-fold) in young panicles correlated with smaller-sized panicles while a mutant LP1 version, lacking this overexpression, correlated with longer panicles (Liu et al., 2016). Reminiscent of the importance of cell-to-cell communication regulation in plant development, the overexpression of the *A. thaliana* transposase DAYSLEEPER was found to induce a more than 65-fold increase in transcript abundance of AtREM6.7. The over- or null-expression of DAYSLEEPER induced very severe developmental defects. These defects included slow growth, no expansion of the cotyledons or development of abnormal flowers and leaves for the null mutants, and delayed flowering, altered cauline leaves, fasciation and partial to total sterility for the overexpressing lines. An intriguing phenotype of the latter lines was reduced petal and sepal growth along with the margins of the sepals appearing petaloid (Bundock and Hooykaas, 2005). These defects could possibly be induced by an alteration of PD conductivity in the meristematic zones considering the known effect of Group 6 REMs on PD conductance (Gui et al., 2014).

# STRUCTURAL AND BIOLOGICAL IMPLICATION OF REM PHOSPHORYLATION

Since the first identification of REM as an *in vitro* phosphorylated protein, pp34 (Farmer et al., 1989), members of all REM groups have been detected in phosphoproteomes from diverse tissues and biological contexts, revealing phosphorylation as a major *in vivo* regulatory mechanism of REMs (see supplementary table 1 for a compilation of REM phosphoproteomic data). A recent study established a phosphorylation pattern of 14 AtREMs in steady-state conditions from 30 different plant tissues (Mergner et al., 2020). Apart from this broad-scale analysis, other studies have shown that, for some residues, the phosphorylation of REMs is modulated by stress conditions such as flg22 and OG treatment, nitrogen deprivation, ABA,H<sub>2</sub>O<sub>2</sub>, cold, osmotic and salt stresses (Benschop et al., 2007; Kohorn et al., 2016; Menz et al., 2016; Nikonorova et al., 2018; Wang et al., 2020, see supplementary table 1), suggesting functional roles of phosphorylation that remain to be explored. Interestingly, most of the phosphorylation has been observed in the N-terminal domain of REMs (Figure 4).

Sequence analysis and in vitro assays showed that AtREM1.3 contains an intrinsically disordered N-terminal region (IDR) (Marín and Ott, 2012). Sequence prediction analysis suggests that most REMs have an IDR in their N-terminal domain (Marín and Ott, 2012). IDR regions are flexible and extended protein segments that provide dynamic structural remodeling and protein-protein interaction plasticity. (lakoucheva et al., 2004; Dyson and Wright, 2005). They are often regulated via protein phosphorylation that may act as a regulatory switch, leading to structural changes such as folding and the sequestration of binding sites (Bah et al., 2015). Because they facilitate multiple protein recognition and binding by acting as adaptable interaction surfaces, IDR regions are often found in hub proteins that link interaction networks and integrate signals (Kim et al., 2008). REMs are found to be phosphorylated in vivo mainly at IDR regions at the N terminus (Figure 4). REMs' basal and signal-induced phosphorylation regions could regulate interactions with its protein partners upon stimulus (Figure 4). This, and the fact that REMs participate in different plant signaling networks, ground the idea that they act as PM-bound-complex signaling "hubs" able to interact with many different proteins, at specific times and locations, and in response to specific stimuli. However, little is known about how REMs integrate diverse signaling cues in plants and how their specific functions are regulated. Only few studies drew a link between REM phosphorylation and intracellular signaling. Marín and Ott. (2012) showed

that AtREM1.3 phosphorylation at S66 located in the IDR region led to a reduced affinity for importins in yeast two-hybrid assays. However, the impact of this phosphorylation on the structure, and subcellular localization of AtREM1.3 remains to be investigated.

Gui et al. (2016) demonstrated that OsREM4.1 is phosphorylated by OsBRI1 to inhibit OsREM4.1 interaction with OsSERK1, leading to OsBRI1-OsSERK1 complex formation and subsequent activation of the brassinosteroid signaling pathway, (Gui et al., 2016, Figure 3B). While the phosphosites remains to be identified, this model connects REM phosphorylation, hormone-signaling balance and rice development, giving an important insight on one of the functional roles of REM phosphorylation in rice.

In Perraki et al. 2018, it was shown that PVX activated kinases responsible for StREM1.3's phosphorylation potentially on S74/T86/S91 sites and that expression of the phosphomimetic but not the phosphoablative mutant of StREM1.3 hampered virus cell-to-cell propagation to similar levels with the WT form Importantly, the calcium-dependent protein kinase AtCPK3, which could phosphorylate StREM1.3 *in vitro* on S74/T86/S91, could also restrict PVX cell-to-cell movement in a REM-dependent manner. This suggests that AtCPK3 orthologue in potato could regulate StREM1.3 *in vivo* for anti-viral defense. Moreover, the phosphorylation mutants had an impact on the localization of REM at PD and on callose deposition, associating phosphostatus, protein mobility, PD permeability and cell-to-cell viral propagation (Perraki et al., 2018, Figure 3C).

Although multiple REM phosphosites have been described in phosphoproteomes or with directed approaches, only few REM-associated kinases have been identified (see supplementary table 1). A recent large-scale phosphoproteomic study identified 8 Arabidopsis kinases (CPK11, MPK6, OST1, SnRK2.4, SOS2, OXI1, CKL2, CRKL2) that could phosphorylate, *in vitro*, AtREM phosphopeptides generated *in vivo* (Wang et al. 2020). Additional kinases responsible for REM phosphorylation have been described in rice, *N. benthamiana*, *M. truncatula*, *L. japonicus* and *A. thaliana* (SnRK1.2, AtCPK3 and various RLKs) (Mehlmer et al., 2010; Tóth et al., 2012; Son et al., 2014; Gui et al., 2016; Perraki et al., 2018; Albers et al., 2019, see a summary Figure 5. However, all these data have been obtained *in vitro* and will require further validation. In particular, *in vivo* interaction by BiFC between REMs and protein kinases has been reported for some of them (Tóth et al., 2012; Perraki et al., 2018; Albers et al., 2019). These kinases can phosphorylate a unique REM or several of them and *vice versa* (Mehlmer et al., 2010; Tóth et al., 2012; Son et al., 2014; Gui et al.,

2016a; Perraki et al., 2018; Albers et al., 2019; Wang et al., 2020) (supplementary Table 1). Interestingly, while most of those kinases are associated with DRMs, (Majeran et al., 2018) some of them are rather soluble, suggesting that DRM association could be triggered by protein interaction, including through REMs.

Indeed REM has been suggested to be a scaffold protein, interacting with several receptor complexes in PM nanodomains (Bücherl et al., 2017; Liang et al., 2018) SYMREM1 (MtREM2.2) interacts with LYK3, NFP and DMI, three Medicago RLKs essential to sense bacterial elicitors (Lefebvre et al., 2010), Figure 3A. These interactions could potentially be a recruiting process of RLKs to specific nanodomains to initiate bacterial symbiosis (Liang et al., 2018). The interplay between REMs and RLKs deserves to be further investigated, considering the fact that they often present overlapping PM-domain localisation and that REM phosphorylation is induced upon stress (Benschop et al., 2007; Kohorn et al., 2016). This capacity of protein-protein interaction through the N-terminal regions presenting highscores of intrinsic disorder, see Figure 4 (Raffaele et al., 2007, Marín and Ott, 2012) and the regulation phosphorylation (Reymond et al., 1996; Marín and Ott, 2012; Gui et al., 2016a; Kohorn et al., 2016; Perraki et al., 2018) are characteristics reminiscent of scaffold proteins, like 14-3-3 family proteins. This analogy holds on the cases where REMs' interaction capacity was reported to differ upon phosphorylation of either the interaction partner(s) or the REM isoform itself (Gui et al., 2016; Liang et al., 2018). 14-3-3 family proteins are involved in phospho-relay events in potentially different ways, preeminently in facilitating and hindering protein-protein interaction by binding to the phosphorylated residues of interaction partners (Lozano-Durán and Robatzek, 2015).

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# **PERSPECTIVES**

The amount of data that has been accumulated since the cloning of the first REM in 1996 on the characteristics and the cellular and physiological role of REMs is very heterogeneous. Although many articles have shown REMs as being involved in a number of physiological processes, either biotic or abiotic, a clear role for the REM family has not yet arose from the ever-increasing amount of data (Figure 1). Nevertheless, many trails have emerged from the 30 years of research on REMs that show great promise in the everlasting search for REMs' functionalities. One of these functionalities stands out, considering the multiple instances

where REMs are linked to intercellular connectivity. These instances reinforce the idea that the establishment of REMs as a genetic family could have been important for the adaptation of photosynthetic algae during the land plant invasion that occurred approximately 475 million years ago (Steemans et al., 2009). Indeed, the control of water and solute exchanges between cells and tissues was a major necessary adaptation in order to handle water fluxes in dry land. The development of complex PD along with a complex vasculature necessary for the establishment of root systems and hormone signaling were the fundamental developments that enabled adaptation and establishment of Embryophytes (Rensing et al., 2008). Moreover, the fact REMs are found to be involved in biotic interactions, notably with symbiotic fungi and bacteria (see section "Plant-Microbe Interactions"), is also a clue to their potential involvement in the conquest of land by plants considering the hypothetical importance of symbiotic microorganisms in helping the first rootless land plants to secure nutrients (for review Rensing 2018).

# 1. Genetics

A major weakness in the functional study of REMs is the lack of genetic tools. To study Group 1 REMs, the most notable problematic is currently the lack of KO-lines for each Group 1 isoform although the generation of these lines is currently ongoing with the recently published CRISPR-Cas9 KO-lines for two Group 1 REMs in *N. benthamiana* (Fu et al., 2018) and the quadruple CRISPR-Cas9 KO-line for all four Group 1 REMs in *A. thaliana* soon available (T. Ott, personal communication). KO lines for each REM Group will be essential for our understanding of the role played by each REM Group that could entail not only different possible cellular functions but also different tissue specificities (*e.g.* Gui et al., 2014). Several REM Groups such as Group 5 and Group 3 could consequently become less illusive as to their function. The generation of KO-lines should be combined with gain-of-function assays as those undertaken in the characterization of OsREM6.6 (or GSD1; Gui et al., 2014) and OsREM4.1 (Gui et al., 2016) in order to develop true functional approaches in deciphering the cellular and physiological purposes of REMs.

# 2. Protein-Protein Interactions

REMs are suspected to be involved in protein-protein interactions considering their N-terminal regions that present high-scores of intrinsic disorder (Raffaele et al., 2007; Marín et al., 2012) and the fact that members of several REM Groups have been found to be phosphorylated (see Figure 3, supplementary table 1). These characteristics are reminiscent of scaffold proteins and notably of 14-3-3 family proteins. Recently, GRF10 (14-3-3 epsilon) was shown to interact with AtREM1.2 and, to be crucial for its partitioning at the PM (Huang et al., 2019). REMs and 14-3-3 family proteins could indeed co-depend on each other considering REMs' interaction capacity was reported to vary upon phosphorylation of either the interaction partner(s) or the REM isoform itself (Gui et al., 2016; Liang et al., 2018;). In both cases, the REM isoforms *i.e.* OsREM4.1 or MtREM2.2 interact with receptor-like kinases (RLKs), OsSERK1 (Gui et al., 2016) and LYK3 and NFP (Liang et al., 2018), respectively (Figure 3). The interplay between REMs and RLKs deserves to be further investigated considering their common phosphorylation and PM-domain association under biotic/stress stimuli (Benschop et al., 2007; Kohorn et al., 2016).

Considering that phosphorylation is at the center of the interaction events recorded for REMs, it seems crucial to develop phospho-dependent interactomic screens for REMs. This advancement would enable us to understand the different phospho-dependent protein-protein interaction regulation levels that are highly probable to occur for many REM isoforms. This type of screen should importantly be performed under different stress conditions and in different tissues as REMs' interactions with its cognate partners appear to be highly determined by plant development and stress.

# 3. The PM's complexity

Important advancements have recently been established in the deciphering of the PM-anchoring properties of REMs (Perraki et al., 2012; Gronnier et al., 2017; Martinez et al., 2018; Legrand et al., 2019), clear problematics have arisen. In as much as REMs are dependent of their C-terminal region or REM-CA for their anchoring to the PM, more must be developed in the understanding of the exact biophysical properties that govern this anchoring. Critically, decrypting the determinants of the PM-nanodomain association of REMs is a top priority, as it has already been shown to be a determining factor of REM function (Gronnier et al., 2017; Fu et al., 2018). In particular, affiliating the presence of

Group 1 REMs in PM-nanodomains with their observed effect on the accumulation of callose at PD pit-fields (Gronnier et al., 2017; Perraki et al., 2018) raises a critical question: how does a protein, present in the PM inner-leaflet, influence enzymatic activities (*i.e.* callose synthesis/degradation) occurring in the cell wall or, at best in the PM outer-leaflet?

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Several hypotheses may be explored to answer this question: 1) Can Group 1 REMs or their interaction partners regulate callose synthases present at PD pit-fields in order to stimulate callose deposition? 2) Can Group 1 REMs or their interaction partners regulate the activity or localization of ß-1,3-glucanases? This latter question can be a particularly interesting hypothesis to investigate considering the different subcellular and extracellular localizations of ß-1,3-glucanases (for review: (Zavaliev et al., 2011). Group 1 REMs could potentially regulate the extracellular secretion of ß-1,3-glucanases as it was reported in Zavaliev et al. 2013 in response to salicylic acid treatments. Yet some ß-1,3-glucanases have been reported to be glycosylphosphatidylinositol (GPI)-anchored proteins i.e. inserted via a lipid moiety within the PM outer-leaflet associated with PD in a tissue-dependent manner (Levy et al., 2007). The enrichment of GPI-anchored proteins in the DRM biochemical fraction (for review on plant GPI-anchored proteins: Yeats et al., 2018) licenses the hypothesis that there could be a form of registration between the inner-leaflet PM-domains containing REMs and the outer-leaflet PM-domains containing GPI-anchored ß-1,3glucanases. In this context, the concept of registration refers to the presence of each component in a common PM-domain that spans from one PM-leaflet to the other. There could therefore be interaction in trans between inner- and outer-leaflet proteins via the interdigitation of very-long-chain acyl chains of the lipids that are present in these PMdomains. This functional mechanism has been demonstrated in animal cells by showing the necessity of phosphatidylserine with a very-long-chain acyl moiety in order to register a GPIanchored protein to a lipid-protein complex that virtually anchored the GPI-anchored protein to the actin cytoskeleton (Raghupathy et al., 2015). More than just a presence in common biochemical fractions, the registration hypothesis is supported by StREM1.3's modification in PM-dynamics under a phosphorylated state (Perraki et al., 2018), hinting to a regulation of StREM1.3's PM-lateral-segregation via the cortical cytoskeleton. This modification in PM-dynamics could possibly modify the PM-dynamics of PM-outer-leafletassociated proteins e.g. GPI-anchored ß-1,3-glucanases. Ultimately, elucidating not only the protein-protein- but also the protein-lipid-interactions necessary for REMs' PM-

nanodomain-association constitutes a great challenge that will participate in the unfurling of the complex and dynamic molecular mechanisms that govern REMs particular role(s) at the PM.

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Considering the fact that REMs of different groups label plethora of PM-domains (Jarsch et al., 2014), new methodologies must be developed in order to study these PM-based events and interactions: these methodologies should include: 1) cutting edge proteomic and lipidomic techniques (e.g. identifying lipids in close interaction with proteins) including phosphoproteomics and the study of lipidated proteins (myristoylation, palmitoylation, isoprenylation, and GPI-anchoring; reviewed in Ray et al. 2017); 2) biophysical tools to study lipid–protein interactions via surface plasmon resonance (e.g. Lenarčič et al. 2017), liposome binding assays and lipid blotting assays (e.g. Perraki et al., 2012), solid-state NMR, Langmuir monolayer tensiometry, and Fourier transform infrared spectrometry (e.g. Gronnier et al., 2017; methods reviewed in Zhou & Hancock 2018); 3) 3D structures of the membranebound interacting complexes including specific lipid-protein complexes by solid-state NMR; 4) generation of mutants impaired in PM-domain-association and the use of superresolution imaging to visualize the in vivo segregation and dynamics of PM-components, which should be a focus in order to better understand the molecular interplay occurring at the protein and lipid clustering sites that are PM-domains. These important tools can considerably be assisted by in silico modeling such as molecular dynamics simulations (for review: Ulmschneider & Ulmschneider 2018). Notably, the study of the PM-bound cancerrelated protein K-RAS is particularly noteworthy as it exemplifies the use of these different methodologies in order to decipher the precise molecular mechanisms underlying K-RAS function (e.g. Zhou et al., 2015; Zhou et al., 2017; Maxwell et al., 2018).

#### **ACKNOWLEDGEMENTS**

This work was sustained by CNRS (Centre National de la Recherche Scientifique) and the University of Bordeaux. This work has benefited from the facilities of the Bordeaux Metabolome/lipidome Facility-MetaboHUB (ANR–11–INBS–0010). AFD, AL, JG and PG were supported by grants from the French Ministère de l'Enseignement Supérieur et de la Recherche (MESR). JG was supported by EMBO LTF 438-2018 and ERC-2017-COG IMMUNO-PEPTALK ID: 773153. SM, BH, MB and VG are supported by ANR project Phospho-REM domain (ANR 2019). SG, SM, VG are supported by ANR project Potymove The IPS2 (MB) benefits from the support of the LabEx Saclay Plant Sciences-SPS (ANR-10-LABX-0040-SPS). BH was supported by the CNRS Momentum.

#### **Author Contributions**

PG and JG developed the rationale of the review and wrote the text with the help of all the co-authors. JG did the phylogenetic analysis (Supp Figure 1). SM did the Figure 1. AL and BH did the Figure 2 and wrote the corresponding text. PG did the Figure 3. AP did the Figures 4 and 5. MDJ and MB gathered the data for the supp table 1 and wrote the corresponding text. AFD and SGR wrote the virus part. SM and VG supervised the writing and figures. All authors read and corrected the manuscript.

#### FIGURE LEGENDS

Figure 1. Cumulative number of articles and reviews dealing directly or indirectly with REMORIN genes since the discovery of REMs in 1984, and the cloning of the first REM in 1996. Source PubMed (https://www.ncbi.nlm.nih.gov/pubmed)

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Figure 2: Molecular driving forces for the formation of StREM1.3-enriched PM nanodomains based on structural analysis. (A) StREM1.3 (blue) clusters at the PM's inner leaflet into nanodomains (red rectangle) enriched in phytosterols and phosphoinositides, the most common being sitosterol and PI4P (Palta et al., 1993, Furt et al., 2010, 2011, Gronnier et al., 2017; Legrand et al., 2019). The overall REM orientation is likely to be perpendicular to the membrane plane to minimize steric hindrance, though the precise angle distribution is unknown. Lipids herein are more ordered than the bulk of the PM and the membrane therefore is slightly thicker even though the PM's complex composition may greatly attenuate this tendency (Gronnier et al., 2018, Legrand et al., 2019). (B) StREM1.3 forms homo-trimers through a coiled-coil domain (Martinez et al., 2018) bundling together three REM C-terminal membrane anchors (RemCA) (Gronnier et al., 2017) and three intrinsically-disordered domains (IDD) bearing phosphorylation sites (Perraki et al., 2018). REM-CA binds to PI4P through electrostatic interactions involving, notably, positively charged amino-acids K192 and K193, as proposed in the right panel by molecular dynamics (Gronnier et al., 2017). The most C-terminal part (region 2) of REM-CA is embedded inside the inner leaflet, as supported by solid-state NMR and molecular dynamics (Gronnier et al., 2017). Nanodomain-associated PIPs being enriched in saturated acyl chains (Furt et al., 2010), sitosterol is also recruited. The left panel shows hydrophobic contacts between the three L155 residues (red), which are critical to the coiled-coil's structure, supporting membrane-association (Martinez et al. 2019). Membrane binding is accompanied by an enrichment in PI4P and sitosterol in the vicinity of the binding site (Legrand et al., 2019). A relative impoverishment in such lipids in the surrounding bulk membrane would therefore be a logical consequence. Note here that only REM molecules are presented, and the other PM proteins are omitted.

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Figure 3. Proposed model for REM-mediated signaling. (A) Group 2 REM in Medicago truncatula. Constitutively-expressed FLOT4 forms a primary PM-scaffold that is unable to recruit LYK3 in the absence of SYMREM1. Nod factor (NF) perception by NFP and LYK3 PM-receptors triggers the activation of a symbiosis-specific signalling cascade that leads to the expression of MtREM2.2. Due to its ability to directly bind LYK3, MtREM2.2 actively recruits the receptor into the FLOT4 domain. In MtREM2.2 mutants, LYK3 is destabilized and endocytosed upon rhizobial inoculation. Illustrations adapted from Liang et al. 2018; (B) Group 4 REM in Oriza sativa. OsREM4.1 protein is PM-localized in association with OsBRI1-OsSERK1 complex. Upon elevetated ABA levels, the ABA-responsive transcription factor OsbZIP23 is activated nd upregulates OsREM4.1 expression. OsREM4.1 protein interacts with OsSERK1 and interferes with OsBRI1-OsSERK1 active complex formation, repressing therefore BR signaling initiation. Increased BR levels, causes the binding of BR to the extracellular domain of OsBRI1 and the activation of OsBRI1 kinase to phosphorylate OsREM4.1. The phosphorylated OsREM4.1, has lower binding affinity to OsSERK1, and therefore the OsREM4.1- OsSERK1 complex is dissociated. Therefore, OsSERK1 is able to interact with OsBRI1 to form the OsBRI1- OsSERK1 receptor kinase complex, and activate BR signaling. OsREM1.4 function is similar to BKI1, which upon BR binding to BRI1, is phosphorylated and released from the PM, allowing the BRI1/SERK complex to form. Illustrations adapted from Gui et al. 2016; (C). Group 1 REM in Nicotiana benthamiana. Proposed model for the molecular mechanisms involved in the StREM1.3-dependent limiting of PVX cell-to-cell movement according to the data from (Raffaele et al. 2009; Perraki et al. 2012; Gronnier et al. 2017; Perraki et al. 2018. Perception of PVX leads to the production of a calcium burst that activatesa group 2 calcium-dependent protein kinase (here CPK3), which in turns phosphorylates group 1 REMs. Group 1 REMs' phosphorylated state increases its PM-mobility and interacts with phospho-REM Interacting Proteins (RIP). These interactions cause an increase in callose deposition at the plasmodesmata.

Figure 4. Phosphorylation of Arabidopsis REMs occurs mostly at Intrinsic disordered regions at its N terminus. Graphs show the intrinsic disorder probability on the Arabidopsis REM proteins that were found to be phosphorylated up to date by *in vivo* studies. *In vivo* phosphorylation site positions on REM sequences are indicated by asterisk. Intrinsic disorder predictions were calculated using the PrDOS-Protein disorder prediction server (http://prdos.hgc.jp/cgi-bin/top.cgi). Coiled-coil predictions were calculated using the COILS program (https://embnet.vital-it.ch/software/COILS\_form.html). REM-CA prediction was estimated based on homology with the REM-CA protein from potato StREM1.3.

**Figure 5. REM proteins are involved in independent signaling pathways and are phosphorylated by different kinases.** Schematic representation of all the known interactions between REM proteins from groups 1, 2, 4 and protein kinases (PK), that were described in plant immunity, symbiosis and hormonal signaling.

#### SUPPLEMENTARY INFORMATION

Figure 1. Phylogenic tree showing the position of the new REM (At1g63295) found in the *A. thaliana* genome. This new REM appears to belong to the group 2, therefore, we named it AtREM2.1.

Table 1: Compilation of phosphoproteomics data sets on REMs of different plant species. (Nühse et al., 2004; Benschop et al., 2007; Niittylä et al., 2007; Nühse et al., 2007; Sugiyama et al., 2008; Whiteman et al., 2008; Li et al., 2009; Reiland et al., 2009; Chen et al., 2010; Grimsrud et al., 2010; Mehlmer et al., 2010; Nakagami et al., 2010; Reiland et al., 2011; Engelsberger and Schulze, 2012; Lan et al., 2012; Mayank et al., 2012; Tóth et al., 2012; Yang et al., 2013; Son et al., 2014; Wang et al., 2014; Choudhary et al., 2015; Hou et al., 2015; Lu et al., 2015; Marcon et al., 2015; Roitinger et al., 2015; Ye et al., 2015; Gui et al., 2016b; Kohorn et al., 2016; Marondedze et al., 2016; Mattei et al., 2016; Nukarinen et al., 2016; Qiu et al., 2016; Vu et al., 2016; Xiang et al., 2016; Qiu et al., 2017; Nikonorova et al., 2018; Perraki et al., 2018; Song et al., 2018; Wang et al., 2018; Albers et al., 2019; Gupta et al., 2019; Wong et al., 2019; Cai et al., 2020; Mergner et al., 2020; Wang et al., 2020)

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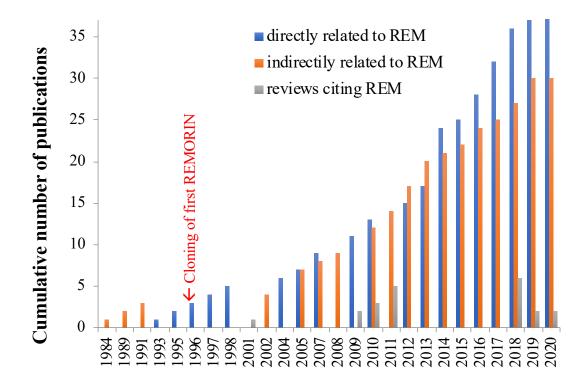
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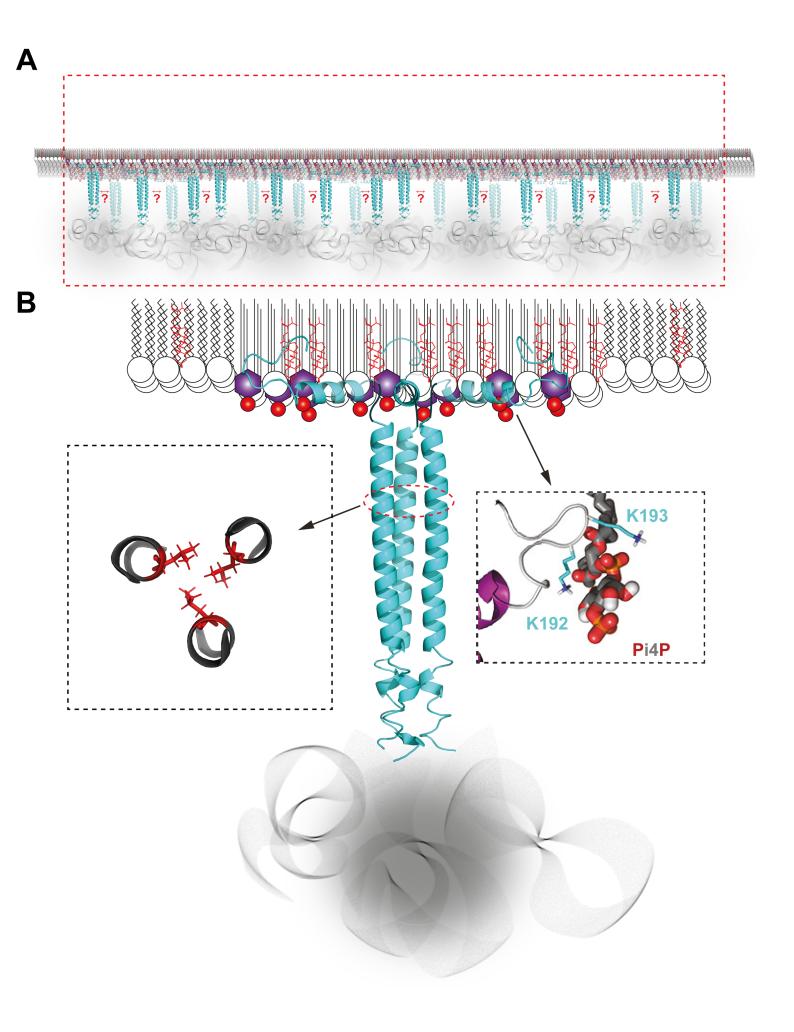
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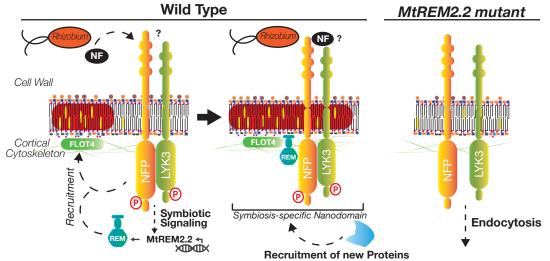
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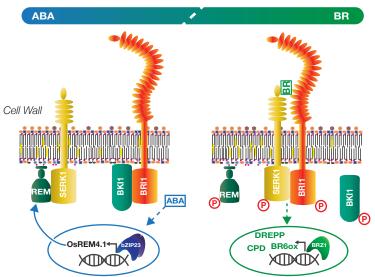




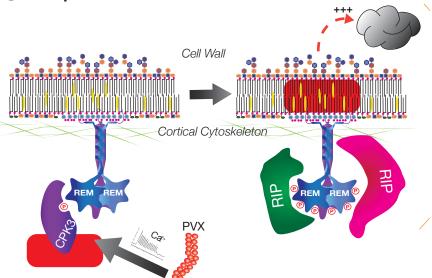
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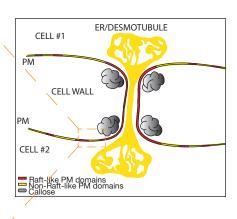


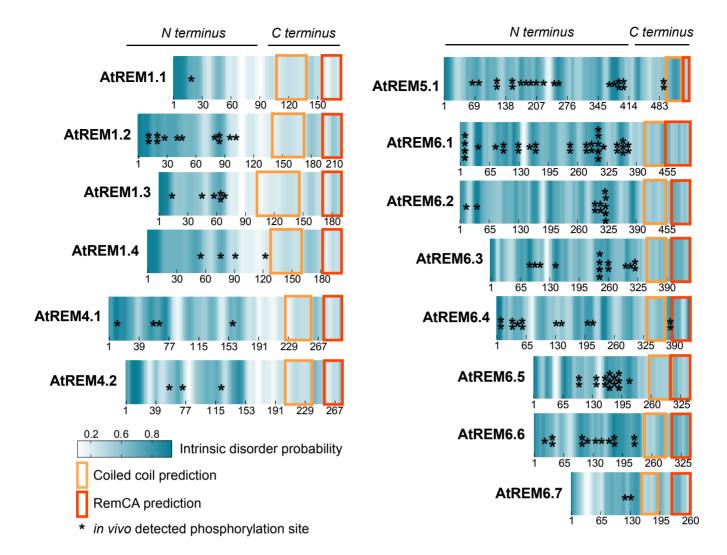
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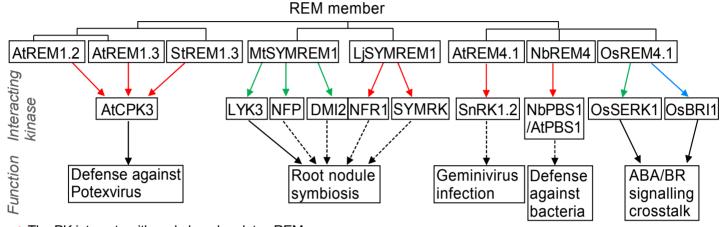


# C Group 1 REM in Nicotiana benthamiana :









- → The PK interacts with and phosphorylates REM
- → The PK phosphorylates REM
- → The PK interacts with REM
- → The PK and REM function together in the biological context
  ---> The PK and REM function in the same biological context but the link of PK/REM in the function is not yet demonstrated

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