

Microreview

Molecular dialogues between viruses and receptor-like kinases in plants

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SUMMARY

Receptor-like kinases (RLKs) play a prominent role in the interaction between plants and extracellular pathogens. Intriguingly, in the past few years several studies have demonstrated that a number of RLKs influence plant susceptibility to viruses and, in some cases, interact with viral proteins. In this review, we will summarize and discuss recent advances suggesting a direct role for RLKs in plant–virus interactions.

Keywords: BAK1, BAM1, BKK1, CLV1, NIK1, receptor-like kinase, virus.

INTRODUCTION

Receptor kinases are proteins localized at the cell surface, formed by an extracellular domain (ECD), a transmembrane domain (TMD), and an intracellular kinase domain (KD). In plants, these proteins are usually known as receptor-like kinases (RLKs) and play an essential role in a multitude of cellular processes, from developmental control to the response to environmental stimuli (Breiden and Simon, 2016; Ye *et al.*, 2017; He *et al.*, 2018). In comparison with other organisms, plants have evolved a notably large family of RLKs, including more than 600 members in *Arabidopsis* and more than 1000 members in rice (Gish and Clark, 2011). The ECDs of plant RLKs are considerably diverse, and may include extensin-like, lectin-like, epidermal-growth-factor-like (including cysteine-rich), lysine motif, and leucine-rich repeat (LRR) domains, among others (Gish and Clark, 2011). RLK ECDs may homo- or hetero-multimerize in order to perceive endogenous or exogenous ligands, including peptides, steroids, oligosaccharides, polysaccharides, and lipopolysaccharides, and transduce these signals to the cell interior (Breiden and Simon, 2016; Ye *et al.*, 2017; He *et al.*, 2018; Smakowska-Luzan *et al.*, 2018), which often results in the initiation of specific intracellular signalling events.

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RLKs play a prominent role in plant–pathogen interactions (Tang *et al.*, 2017). Some RLKs have been shown to act as pattern-recognition receptors (PRRs), mediating the perception of molecular patterns of plant or microbial origin, usually termed damage-associated molecular patterns (DAMPs) or pathogen-associated molecular patterns (PAMPs), respectively (Zipfel, 2014). These molecular patterns are usually recognized as danger signals by plant cells, leading to the activation of immune responses (Macho and Zipfel, 2014) and the subsequent development of pattern-triggered immunity (PTI). Other RLKs have been found to interact with PRRs, providing a scaffold for their association with other proteins or regulating the activation of signalling (Tang *et al.*, 2017; Smakowska-Luzan *et al.*, 2018). Additionally, non-PRR RLKs may also contribute to the plant response to pathogen perception by regulating molecular cross-talks or developmental rearrangements associated with immunity (Tang *et al.*, 2017).

While the importance of RLKs, especially PRRs, in plant defence against bacteria, fungi, oomycetes, and even insects is widely accepted, their contribution to plant–virus interactions is currently under debate. In principle, a potential role of RLKs in the perception of invading viruses seems counterintuitive, since these proteins relay signals from the extracellular space, while viruses are intracellular pathogens; consistently, RNA interference (RNAi) is considered the main antiviral defence mechanism (Yang and Li, 2018). However, it cannot be excluded that the viral infection could result in the release to the apoplast of tell-tale molecules, either derived from the virus itself (proteins or nucleic acids) or as a result of cellular damage or the activation of plant defence mechanisms (DAMPs) (Fig. 1). Additionally, RLKs involved in the regulation of developmental processes and hormonal responses might have an indirect impact on the viral infection, hence contributing to the final outcome of the interaction between virus and host; due to space limitations, RLKs with no known role in plant defence and not described as targeted by viruses will not be discussed in this review (Fig. 1). Interestingly, recent works have unveiled that a number of RLKs indeed influence

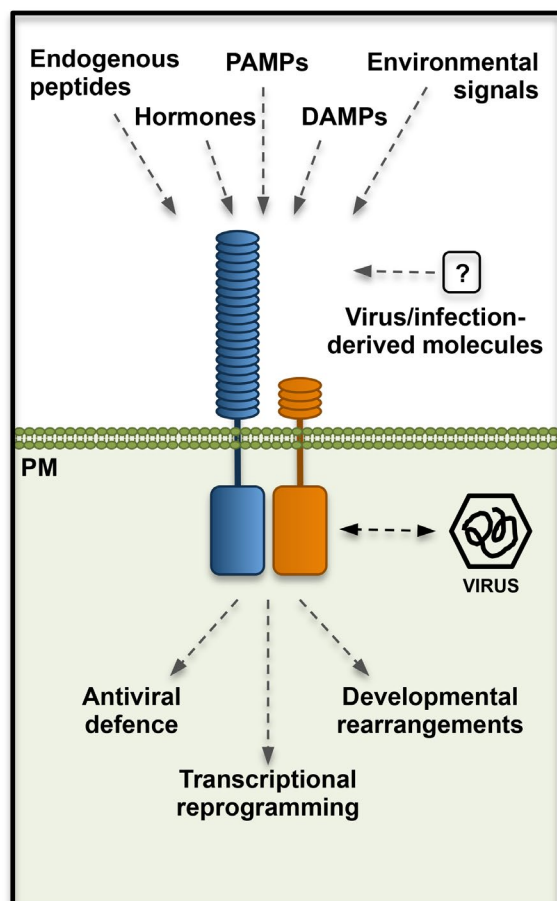


Fig. 1 Extracellular signals potentially perceived by RLKs and potential outcomes with an impact on plant–virus interactions. These signals may include not only molecules from plant or pathogen origin, but also environmental cues. PM, plasma membrane.

plant susceptibility to viruses, in some cases being direct targets of viral proteins (Korner *et al.*, 2013; Zorzatto *et al.*, 2015; Gouveia *et al.*, 2016; Niehl *et al.*, 2016; Calil and Fontes, 2017; Carluccio *et al.*, 2018; Li *et al.*, 2018; Rosas-Diaz *et al.*, 2018); some of these RLKs are well-known players in plant immunity, while others may exert novel functions in antiviral defence (Fig. 2).

Potential role of RLK-mediated PAMP- or DAMP-triggered immunity in antiviral defence in plants

Somatic embryogenesis receptor kinases (SERKs) are a small group of LRR RLKs that act as co-receptors for multiple receptor kinase complexes, including those formed by most LRR-containing PRRs identified to date, playing a major role in the activation of PTI triggered by PAMPs or DAMPs (Ma *et al.*, 2016). SERK3/BRI1-ASSOCIATED KINASE 1 (BAK1) is possibly the member of this family making the largest

contribution to PTI (Ma *et al.*, 2016). Importantly, a role for BAK1 in antiviral defence was demonstrated by Yang *et al.* (2010) and, later, by Korner *et al.* (2013), who showed that a *bak1* Arabidopsis mutant displayed increased susceptibility to three unrelated RNA viruses, namely *Oilseed rape mosaic virus* (ORMV) (genus Tobamovirus), *Tobacco mosaic virus* (TMV) (genus Tobamovirus), and *Turnip crinkle virus* (TCV) (genus Carmovirus); mutation in the closest BAK1 homologue, SERK4/BKK1, also results in enhanced TCV accumulation (Yang *et al.*, 2010). Interestingly, infection by these viruses induces the expression of the DAMP propeptide-encoding *ProPEP2* and *ProPEP3*, which in turn produce the immune peptide Pep1, as well as the expression of the genes encoding the Pep1 receptors, *PEPR1/2*, which use BAK1 as co-receptor (Schulze *et al.*, 2010; Postel *et al.*, 2010). However, lack of *PEPR1/2* did not affect viral accumulation, suggesting that it is the contribution of BAK1 to a signalling pathway other than *PEPR1*-mediated PTI what increases viral resistance. Another interesting finding is that crude TCV viral extracts, but not purified virions, induce hallmark PTI readouts (MAPK activation, ethylene production, and inhibition of root growth) in a BAK1-dependent manner (Korner *et al.*, 2013), which hints at the existence of an infection-derived molecule perceived by a BAK1-containing receptor complex (Fig. 1). This is further supported by the observation that viral infections often result in the induction of PTI-related genes (Whitham *et al.*, 2003; Love *et al.*, 2005; Carr *et al.*, 2010; Hanssen *et al.*, 2011; Nicaise and Candresse, 2017), and by the discovery of at least two viral proteins, the capsid protein (CP) from *Plum pox virus* (PPV) (genus Potyvirus) and the movement protein (MP) of *Cucumber mosaic virus* (CMV) (genus Cucumovirus), with PTI-suppressing activity (Nicaise and Candresse, 2017; Kong *et al.*, 2018). That suppressing PTI could be beneficial for an invading virus is not inconceivable, since the activation of PTI results in multiple outputs associated with plant defence, some of which may have a negative effect on the viral infection: at least in some cases, accumulation of reactive oxygen species (ROS) can have a deleterious effect on the viral invasion (Wu *et al.*, 2017), and the activation of salicylic acid (SA) signalling has proven effective against a plethora of different plant viruses (reviewed in Alazem and Lin (2015)). Additionally, and since most plant viruses are transmitted by insect vectors, indirect effects on viral propagation should also be considered.

More challenging perhaps is to imagine what kind of viral molecule could act as a PAMP, given that a general feature of PAMPs, according to the accepted definition, is their high degree of conservation due to strong evolutionary constraints, while viral proteins mutate at a high speed – a property that underlies the limited durability of any sequence-based antiviral resistance strategy. In this scenario, it seems more likely that if a viral PAMP exists, this is a conserved structure that

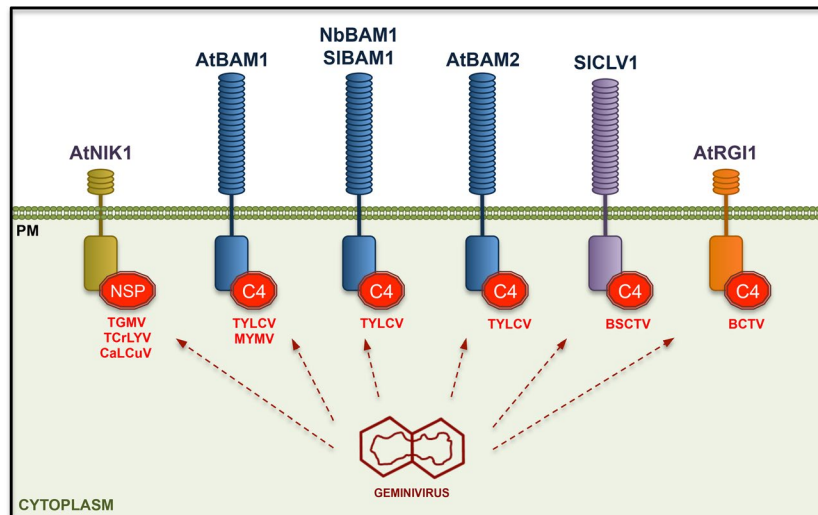


Fig. 2 RLKs are targets of viral proteins. Different proteins from plant viruses interact with RLKs, including the specific plant and virus species employed in the corresponding studies. TGMV, *Tomato golden mosaic virus* (TGMV); TCrLYV, *Tomato crinkle leaf yellow virus* (TCrLYV); CaLCuV, *Cabbage leaf curl virus*; TYLCV, *Tomato yellow leaf curl virus*; BSCTV, *Beet severe curly top virus*; BCTV, *Beet curly top virus*.

can be recognized as non-self, rather than a specific protein/peptide/nucleic acid sequence (Fig. 1). Alternatively, it could be virus-induced DAMPs which activate PTI-like responses, likely through their perception by PRR complexes that involve BAK1.

Interestingly, double-stranded RNA (dsRNA) (or the dsRNA analog poly(I:C)) has been shown to trigger PTI-like responses in both *Arabidopsis* and *Nicotiana benthamiana* (Niehl *et al.*, 2016). Since dsRNA is generated during viral infections (as the viral genome itself, replicative intermediates, or as the result of the activation of antiviral gene silencing), but is not abundant in the plant cell in uninfected conditions, dsRNA would be a good candidate to be recognized as a signal of the viral invasion and be considered a viral PAMP. Nevertheless, perception of dsRNA/poly(I:C) depends on SERK1, and not on BAK1 or BKK1, which suggests that the previously observed involvement of the latter in antiviral defence relies on a different pathway (Yang *et al.*, 2010; Korner *et al.*, 2013; Niehl *et al.*, 2016); whether SERK1 has a general antiviral role remains to be determined. Additionally, whether perception of dsRNA is intracellular or extracellular, and, in the latter case, how the virus-derived molecules would reach the apoplast in sufficient amounts to be detected, is still unclear.

Taken together, and although fragmentary, previous work suggests that plant viruses might be both targets and suppressors of PTI or PTI-associated responses. However, at present, alternative options cannot be excluded. For example, BAK1 contributes to several other RLK-mediated signalling pathways (Ma *et al.*, 2016) and has been shown to regulate jasmonic acid

(JA) content in *Nicotiana attenuata* (Yang *et al.*, 2011); this or a similar, yet unknown, role of BAK1 on other, non-PTI-related pathways may underlie its effect on the viral infection. The viral susceptibility phenotype of mutants in other PTI components is inconsistent (Korner *et al.*, 2013; Nicaise and Candresse, 2017), which may nevertheless reflect different virus invasion strategies. A more systematic, comprehensive analysis, including RNA and DNA viruses belonging to different families, will be required to gain a global overview of the potential interplay between plant viruses and PTI responses.

Receptor-like kinases targeted by viral proteins

In recent years, perhaps unexpectedly, several RLKs have been identified as direct targets of viral proteins (Fig. 2), and this number is likely to increase in the near future. In some cases, the biological function of the targeted RLK in plant–virus interactions has been unveiled, while in others it remains elusive, but whether these proteins are acting as receptors of extracellular cues during the viral infection is an open question common to all of them.

The first RLKs to be identified as interactors of a viral protein were *Arabidopsis* NSP-INTERACTING KINASE 1, 2, and 3 (AtNIK1-3), which are bound and inhibited by the nuclear shuttle protein (NSP) of bipartite geminiviruses (*Tomato golden mosaic virus* (TGMV), *Tomato crinkle leaf yellow virus* (TCrLYV), and *Cabbage leaf curl virus* (CaLCuV)) (Fontes *et al.*, 2004). Interestingly, plasma membrane-localized AtNIK1 initiates a novel antiviral response in plants, mediated by the ribosomal protein RPL10a, which results in the translational shutdown of viral genes and

is suppressed by the viral NSP (Carvalho *et al.*, 2008; Rocha *et al.*, 2008; Zorzatto *et al.*, 2015). Still to be elucidated are the mechanisms employed by monopartite geminiviruses, which lack an NSP, as well as viruses belonging to other families, to interfere with this signalling cascade. Of note, AtNIK1 interacts with AtBAK1 (Smakowska-Luzan *et al.*, 2018), raising the possibility that the previously observed contribution of AtBAK1 to antiviral immunity relies on this pathway and not PTI. However, considering that both AtNIK1 and AtBAK1 belong to the same subfamily of LRR-RLKs (subfamily II) in Arabidopsis, and share a similar structural organization (Shiu and Bleecker, 2001), a role for NIK1 as a co-receptor or signalling partner for other RLK(s) should not be ruled out.

Another geminiviral protein, C4/AC4, has been recently shown to bind RLKs in the CLAVATA 1 (CLV1) clade (reviewed in Zeng *et al.* (2018)). C4 from *Tomato yellow leaf curl virus* (TYLCV) and *Mungbean yellow mosaic virus* (MYMV) interacts with Arabidopsis BARELY ANY MERISTEM 1 (AtBAM1) and, at least in the case of TYLCV, its close homologue AtBAM2 (Carluccio *et al.*, 2018; Rosas-Diaz *et al.*, 2018). C4 from TYLCV also interacts with the BAM1 orthologs from tomato and *N. benthamiana* (Rosas-Diaz *et al.*, 2018). The interaction between C4 and BAM1/2 is particularly strong at plasmodesmata (PD) and, strikingly, BAM1/2 seem to be required for the cell-to-cell spread of RNA interference (RNAi) from the vasculature, a function suppressed by C4 (Carluccio *et al.*, 2018; Rosas-Diaz *et al.*, 2018). Since RNAi is considered a key antiviral mechanism in plants, it is tempting to speculate that BAM1/2 or other components involved in the spread of RNAi through the PD will be convergently targeted by proteins encoded by diverse viruses, something that remains to be seen. However, it is worth noting that, at present, an alternative function of BAM1/2 on the viral infection, e.g. in viral movement through the PD, cannot be excluded.

The C4 protein from *Beet severe curly top virus* (BSCTV), on the other hand, can interact with SICLV1, and this has been suggested to potentially underpin symptom development (Li *et al.*, 2018); however, the functional relevance of this interaction is still poorly understood. Interestingly, C4 from yet another geminivirus, *Beet curly top virus* (BCTV), was previously found to bind the Arabidopsis RLK RGF INSENSITIVE 1 (AtRG1) (Piroux *et al.*, 2007), although this interaction was not characterized further. Taken together, these results suggest that geminivirus C4 might target an array of phylogenetically related RLKs (Zeng *et al.*, 2018), although the number and significance of these intriguing interactions would need to be globally addressed.

Outlook

A growing body of data generated in the past few years seems to point at a potential role of RLKs in plant–virus interactions, which may occur at different levels: RLKs may mediate antiviral

PTI-like or alternative defence responses, activate developmental pathways re-wired by the viral infection, or facilitate the cell-to-cell movement of antiviral signals or the virus itself, among other things. Nevertheless, the results currently available in the literature are rather fragmentary and getting a global overview of how different RLKs contribute to the viral infection will necessarily require a more comprehensive and integrative approach, in which viruses belonging to different families, with diverse replication and transmission strategies, are tested and compared. Additionally, and since fast evolution makes viral proteins excellent probes for plant functions, the identification and study of RLKs targeted by viruses might help uncover new roles of RLKs with an impact on the viral invasion of the plant – a potentiality that has already materialized in the novel functions uncovered for NIK1 and BAM1/2.

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