



Influence of virus–host interactions on plant response to abiotic stress

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Abstract

Environmental factors play a significant role in controlling growth, development and defense responses of plants. Changes in the abiotic environment not only significantly alter the physiological and molecular pathways in plants, but also result in attracting the insect pests that carry a payload of viruses. Invasion of plants by viruses triggers the RNA silencing based defense mechanism in plants. In counter defense the viruses have gained the ability to suppress the host RNA silencing activities. A new paradigm has emerged, with the recognition that plant viruses also have the intrinsic capacity to modulate host plant response to environmental cues, in an attempt to favour their own survival. Thus, plant–virus interactions provide an excellent system to understand the signals in crosstalk between biotic (virus) and abiotic stresses. In this review, we have summarized the basal plant defense responses to pathogen invasion while emphasizing on the role of RNA silencing as a front line of defense response to virus infection. The emerging knowledge indicates overlap between RNA silencing with the innate immune responses during antiviral defense. The suppressors of RNA silencing serve as Avr proteins, which can be recognized by the host R proteins. The defense signals also function in concert with the phytohormones to influence plant responses to abiotic stresses. The current evidence on the role of virus induced host tolerance to abiotic stresses is also discussed.

Keywords Abiotic stress · Effector-triggered immunity · Pattern-triggered immunity · RNA silencing · Suppressors of silencing · Virus infection

Introduction

The sessile nature of plants makes them more prone to stress caused by environmental perturbations and attacks by various pathogens. High temperatures exert abiotic stress and can also result in an increase in the incidence of insect vectors that carry with them a load of pathogens. Amongst all pathogens, viruses being obligate parasites can replicate

only inside living cells and are responsible for imparting number of diseases in animals and plants. Viruses are present in almost every ecosystem and biological entity and piggy bank on insects for their transmission and spread in plants (Gallet et al. 2018). They invade normal host cells and hijack the cellular machineries for their own replication and multiplication. Virus infected plants often show severe abnormalities like stunting, leaf curling, leaf mosaic pattern, necrosis, chlorosis, wilting etc. (Hull 2009). All these deformities have drastic effects on crop productivity and quality leading to substantial agricultural losses (Dawson and Hilf 1992).

In order to protect themselves, plants have developed sophisticated defense mechanisms, which are both unique and overlapping. Substantial progress has been made in identifying the key stress-responsive genes associated with individual stresses, yet relatively little information is available on the crosstalk in response to combined stresses, specifically the interactions between biotic and abiotic stress responses. The present scenario of climate change is predicted to have a negative impact on biotic stress resistance

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in plants (Chattopadhyay et al. 2019). Therefore, it is vital to identify the common abiotic stress- and pathogen-specific genes that confer multiple stress tolerance in plants. Here, we discuss the recent advances in understanding the common molecular mechanisms that operate in response to virus infection and abiotic stresses.

Understanding plant immunity

Plants, like all other organisms, have a sophisticated natural defence mechanism by which they are able to distinguish between self and nonself molecules (Wu et al. 2014). Their primary defences can be grouped into two broad categories viz. constitutive and induced. The constitutive defences include the structural barriers like cuticles, thorns, trichomes, cell wall etc. and chemical barriers formed by the deposition of lignin, callose, glucosinolates, saponins (phytoanticipins), terpenoids, phenolics etc. (Freeman and Beattie 2008; Moreira et al. 2012). Initial defense responses also include alkalization of medium due to change in concentrations of H⁺, K⁺ and Ca²⁺ ions across the plasma membrane (Jabs et al. 1997). Elevation of cytoplasmic Ca²⁺ also serves as a signal for generation of reactive oxygen species (ROS), production of salicylic acid (SA) and closure of stomata (Nomura et al. 2008; Carr et al. 2010).

The induced defenses are activated during infection to orchestrate transcriptional reprogramming using the basal defense systems (Dodds and Rathjen 2010; Tsuda and Katagiri 2010) viz. Pathogen associated molecular pattern triggered immunity (PTI) and effector triggered immunity (ETI). The presence of PTI limits pathogen growth and puts selective pressure on them to invade the host cells (Thomma et al. 2011). Successful pathogens have evolved to produce different types of virulence factors or effectors for suppressing PTI. In retribution, the host have also evolved to produce specific R-proteins that can recognize the effectors and ETI comes into play. In case, the pathogen is able to secrete effectors that are not detected by the R-proteins, they cause effector triggered susceptibility (ETS) and become virulent. This sequence of events is best explained by the Zig-Zag model (Jones and Dangl 2006).

The concept of PTI and ETI is still not clear in case of viral pathogens as they can invade the cells through plasmodesmata connections. However, the viral double stranded RNAs (dsRNAs) are generally paralleled to the PAMPs as they not only trigger the RNA silencing pathways but also activate the PTI signalling. Similarly, the virus encoded RNA silencing suppression activity corresponds to the effectors that are recognized by the R proteins to activate the ETI pathways. The following sections provide a brief overview on the plant immune pathways and their overlap

during viral infections has been discussed in [RNA silencing shield against virus infection](#).

PAMP triggered immunity

It is the basal defense response or first line of defense response triggered by the recognition of special molecular patterns on the surface of microbes like viruses, bacteria and fungi. The Pathogen Associated Molecular Patterns (PAMPs) or Microbe Associated Molecular Patterns (MAMPs) are indispensable parts of pathogen (Zhang and Zhou 2010). The PAMPs/MAMPs act as elicitors of defense responses in host cells and are highly conserved across large groups of pathogens (Table 1). The elicitors may be classified as exogenous or endogenous based on their origin (Zipfel 2014). This is best exemplified by cell wall degradation products, as they may be exogenous when plants enzymes like chitinase lead to fungal cell wall degradation or may be endogenous when microbial cellulases lead to the degradation of plant cell wall (Weinberger and Friedlander 2000).

The PAMPs/MAMPs are recognized by pathogen recognition receptors (PRRs), which are normally members of the receptor like kinases (RLKs) and Receptor like protein kinases (RLPs) present on the cell membrane (Goff and Ramonell 2007). PRRs are structurally similar to toll-like receptors (TLRs) that are found in animals (Kopp and Medzhitov 2003). The binding of PAMPs/MAMPs to the PRRs triggers a signalling cascade, which results in rapid oxidative burst due to the production of ROS (Daudi and O'Brien 2012), activation of MAPKs (Schwessinger and Rathjen 2015), formation of callose (Ellinger and Voigt 2014) and expression of defense related genes like those coding for PR proteins (Zhang et al. 2019; Paludan et al. 2021).

It was shown that, binding of Flg22 (Flagellin derived 22; a PAMP) to FLS2 (a PRR) leads to phosphorylation of the kinase domain of FLS2 (Gomez-Gomez et al. 2001). The phosphorylated FLS2 dimerizes with BAK1 (Brassinosteroid insensitive 1 (BRI-1) associated kinase 1) and BIK1 (Botrytis-Induced Kinase 1) to trans-phosphorylate BIK1 (Chinchilla et al. 2007). The addition of phosphate group causes a conformational change and BIK1 is released (Wang et al. 2012). The *fls2* mutant Arabidopsis plants are unable to respond to flg22 and this leads to avoidance of PTI (Gomez-Gomez and Boller 2000). In *Arabidopsis* BIK1 triggers the MAP kinase pathway, which leads to activation of WRKY transcription factors (Pandey and Somssich 2009). The WRKY proteins interact with W-box (TTGACC/T) motif in promoter of defense related genes (Navarro et al. 2006). BAK1 also contributes to antiviral resistance (Kørner et al. 2013) and this is discussed in [RNA silencing shield against virus infection](#).

Table 1 List of elicitors and receptors associated with PTI

Microbes	PAMPs/MAMPs (elicitors)	PRRs/RLPs (receptors)	References
Bacteria	Flagellin, flg22	FLS 2	Sun et al. 2012
	EF-Tu	EFR	Zipfel et al. 2006
	Peptidoglycan & Lipopolysaccharide	Lysine motif containing proteins	Xu et al. 2017
	Lipopolysaccharide (LPS)	Lipo oligosaccharides specific reduced elicitation (LORE)	Ranf et al. 2015
	Cold Shock protein (csp22)	Cold shock protein receptor (CORE) and RLP required for CSP22 responsiveness (CSPR)	Wang et al. 2016; Saur et al. 2016
	XA 21	Rax XST	Pruitt et al. 2015
	XPS1	Xanthine/Uracil permease (xup25 epitope)	Mott et al. 2016
	Extracellular polysaccharide	EPR3	Wong et al. 2020
	nlp 20	RLP 23	Albert et al. 2015
	Fungi	Chitin	CERK 1
		Chitin Oligosaccharide Elicitor Binding Protein (CEBiP)	Kaku et al. 2006
Beta- glucans		dectin-1 (CLEC 7A)	Brown et al. 2002
Ethylene inducing xylanase (EIX)		Eix1 & Eix 2	Ron and Avni 2004
Avr4E		Hcr9-4 EB	Westerink et al. 2004
Virus	Avr 2,4,5	eLRR or Cf genes (<i>Cladosporium fulvum</i>)	Zhao et al. 2019a, b
	dsRNA	Actual Receptor is not known, but BAK1 related SERK1 complex is involved in signalling	Niehl et al. 2016
Endogenous molecular patterns	Oligogalacturonide (released from plant cell wall)	Wall associated Kinases	Brutus et al. 2010
	PIP 1	RLK7	Hou et al. 2014

Effector triggered immunity

Recognition of PAMPs by PRRs puts selection pressure on pathogens to evolve strategies for escaping from host plant detection. The evolution of noneliciting PAMPs is one way by which the pathogen can overcome host resistance. This is best exemplified by Flg15, which is short version of Flg22 and is fully active in tomato while it does not act as elicitor in *Arabidopsis* (Robatzek et al. 2006). Another strategy involves modification of the PAMPs by post-translational modification to escape from recognition (Taguchi et al. 2009). For example the defense response is higher in response to nonglycosylated Flagellin when compared with the glycosylated one.

The pathogens also produce virulence factors called effectors to evade the PTI (Ranf 2018) and the efficiency of the effector proteins determines the pathogenicity. In bacteria, the effector proteins are produced via type 3 secretion system, from a set of *avr* genes. The AVR effectors can be detected by the host encoded resistance (R) proteins (Jones and Dangl 2006). Majority of R-proteins contain NB-LRR (NB- nucleotide binding at N-terminal, LRR- leucine rich repeats at C-terminal) domains (de Ronde et al. 2014a). These proteins not only provide an early warning system but also activate further immune signalling. The NB-LRR proteins are very useful for identifying host and nonhost effectors. If the products of dominant allele of *avr* gene

and dominant allele of *R* gene interact then disease will not occur, due to activation of ETI, which are stronger than PTI and include genes that confer resistance against virus also.

Host resistance response

ETI response is associated with an acquired Host Resistance (HR) response which is a localised mechanism of programmed cell death (PCD) to confine or restrict the virulent pathogen in particular area (Fu and Dong 2013; Lee and Yeom 2015). Phenotypically it is manifested as necrosis and is initiated when the interaction of pathogen-AVR proteins with the host R-proteins. This interaction leads to the production of various kinds of ROS, of which H₂O₂ is the most stable and common type involved in cell death. The pathogen induced oxidative burst leads to oxidative mutagenesis of DNA and other cellular damage. Many biotrophic pathogens like *Puccinia striiformis* try to overcome host generated ROS while the necrotrophic pathogens like *Botrytis cinerea* utilise ROS for their own benefits. Some pathogenic fungi use hyphal growth to conduct PCD for obtaining nutrition from dead cells while others use it as a direction cue during invasion (Singh et al. 2021).

Local pathogen infection also triggers the SAR (Systemic Acquired Resistance), which provides a general resistance to the whole plant. It is conferred by co-ordinately induced production of SA and the expression of PR proteins. SA inhibits

the catalase activity and adds to the elevation of the cellular levels of H₂O₂. This system also serves as a mechanism to generate long lasting immune memory whose duration may vary with time and is boosted by repeated infections. Transgenic plants that produce excessive amounts of SA degrading enzyme, salicylate hydroxylase and SA mutants were defective in SAR (Fu and Dong 2013).

The SAR also results in transcriptional reprogramming through the NPR1 (Non expressor of PR genes). The over-expression of NPR1 results in broad-spectrum resistance while *npr1* mutants are susceptible to infection. The NPR1 domain has 10 conserved cysteine residues, which help in binding to the SA molecule (Noctor et al. 2002; Vanacker et al. 2000). During infection the gradual elevation of SA alters the redox potential and releases the NPR1 monomers which then move into nucleus and bind with TGA transcription factors to induce PR gene expression (Fu et al. 2012). In healthy tissue, SA is conjugated and partitioned in vacuoles and NPR1 is bound by NPR4, which leads to its degradation by 26 proteasome complex.

Non host resistance response

Every plant is not affected by the same pathogen because of the one sided evolution. In this context, Non host resistance (NHR) has emerged as a common and most durable type of resistance. The use of one or more proteins (Table 2) for the detection of effectors of nonadapted pathogens leads to the

induction of ETI in NHR (Lee et al. 2017). The NHR acts as a kind of outermost layer, which includes preinvasion and postinvasion responses. The preinvasion response, which can be either passive or active, restricts pathogens from entering into plant while the postinvasive response is the active defense response, which triggers HR.

RNA silencing shield against virus infection

The mechanism of RNAi (RNA interference) or RNA silencing constitutes another line of defense that is activated in response to infections by virus and some bacteria. It helps plants to defend themselves from viral infections and develop memory after reinfection by the same or closely related viruses (Sanan-Mishra et al. 2021). It can operate through post translational gene silencing (PTGS) and transcriptional gene silencing (TGS) (Liu and Chen 2016; Sinha et al. 2017; Song et al. 2019). In PTGS, foreign or aberrant dsRNA is recognized by a microprocessor complex and is converted in to 21–24 nucleotide small RNAs by the action of Dicer-like (DCL) protein (Brant and Budak 2018; Singh et al. 2019). These small RNAs get incorporated in to the RISC (RNA Induced Silencing Complex) and guide it to the target mRNAs in a sequence dependent manner, where it is cleaved by the Argonaute (AGO) protein present in this complex (Sanan-Mishra et al. 2021). In plants, the small RNAs can be further amplified by host encoded RNA dependent

Table 2 List of proteins involved in Non host resistance responses

S.No	Protein	Function	References
Pre-invasive response			
1	BRT1	Bright trichomes (UDP glycosyltransferase)	Langenbach et al. 2013
2	CSLD2	Cellulose synthase-like D2 gene (Regulator of cell wall cellulose)	Douchkov et al. 2016
3	EAS/EAH	Involved in phtoalexin Biosynthesis	Lee et al. 2017
4	PEN1	Syntaxin vesicle targeting protein	Collins et al. 2003
5	PEN2	Glycosyltransferase	Lipka et al. 2005
6	PEN3	ATP-binding cassette (ABC) transporter	Stein et al. 2006
Postinvasive response			
1	ELO1 ELO2	Elongator complex (involved in leaf/root development)	An et al. 2017
2	NHO1	Glycerol metabolism	Kang et al. 2003; Lu et al. 2001
3	SAG101	Senescence associated gene 101	Lipka et al. 2005
4	SGR	Chlorophyll catabolism	Ishiga et al. 2015
5	SQS	Biosynthesis of phytosterol	Wang et al. 2012
Involved in both types of responses			
1	EDR1	Negative regulator of cell death	Frye et al. 2001; Hiruma and Takano 2011
2	EDS	Enhanced Disease Susceptibility (lipid metabolism)	Moreau et al. 2012
3	PSS1	Glycine-Rich protein	Sumit et al. 2012

RNA polymerases resulting in amplification and spread of the RNA silencing response (Baulcombe 2004; Qiao et al. 2013; Sanan-Mishra et al. 2021). In TGS pathway the small RNAs are incorporated into RITS (RNA Induced Transcriptional Silencing) complex to guide the inactivation of target DNA by methylation and heterochromatinization (Muthamilarsan and Prasad 2013).

The small RNAs, frequently known as noncoding RNAs, have been broadly classified as short-interfering RNAs (siRNAs) and microRNA (miRNAs) based on their biogenesis and function (Table 3). siRNAs are produced from long dsRNAs that may arise either from endogenous sources like transposons, repetitive elements and centromere (Kumar et al. 2014; Chowdhury 2019) or exogenous sources like invading viruses or aberrant inverted repeats. These can be subclassified as repeat-associated siRNA (ra-siRNA), trans-acting siRNA (ta-siRNA), natural-antisense siRNA (nat-siRNA), heterochromatic siRNA (hc-siRNA) and viral siRNAs (vi-siRNA). It is largely considered that siRNA formation influences resistance to virus infection, suppression of transgene expression and inactivation of transposon action (Sanan-Mishra et al. 2021). The miRNAs are produced endogenously from genome coded hair-pin or stem-loop RNA. They are present as large families and regulate almost every aspect of plant growth, development and response to stress (Waititu et al. 2020). Extensive overlap and redundancy exists between the small RNA pathways for intricately regulating the plant responses.

The role of RNA silencing during virus infection has been well elucidated and the term virus induced gene silencing (VIGS) was specifically coined to explain the phenomenon of recovery from virus infection (Van Kammen 1997). In fact viral vectors have been used to knock down expression of endogenous host genes to assess gene functions and raise virus resistant plants. Infection by viruses triggers the production of local primary small RNAs as well as systemic or transitive secondary small RNAs. In primary silencing, the viral dsRNAs are recognised and processed into siRNAs mainly by the action of DCL4. In secondary silencing, the single stranded viral transcripts are acted upon by RDR6 and SGS3 to produce dsRNA. This process is primed by the primary siRNAs and the dsRNAs thus generated are processed by DCL2 or DCL4 to produce the transitive siRNAs (Sanan-Mishra et al. 2021).

Viral dsRNA act as elicitors

The viral dsRNA, act as elicitors to trigger RNA silencing and PTI. Majority of plant viruses replicate via dsRNA intermediate, which may serve as the principal inducer of the siRNA. The secondary structure or convergent transcription of viral RNAs can also serve as a potent trigger for the RNA silencing pathway. The dsRNAs are recognized

Table 3 Features of various classes of plant small RNAs

Small RNA	Size (nt)	Source of dsRNA	Mode of action	Main Function	References
ra-siRNA	24	Genomic repeats and retrotransposons	Chromatin modification (TGS)	Silencing of repetitive genes and transposons	Singh et al. 2019
hc-siRNA	23–24	Intergenic and/or repeat regions	Regulation of chromatin modification (TGS)	Genome stability	Chellappan et al. 2010; Fei et al. 2013
ta-siRNA	21–22	Transposable elements, noncoding TAS/PHAS gene transcripts	DNA methylation (TGS) or transcript cleavage (PTGS)	Plant development and stress response	Adenot et al. 2006; Vaucheret 2006; Johnson et al. 2009; Allen and Howell 2010;
pha-siRNA	21–24	Independently transcribed complementary mRNAs	Transcript cleavage or Translational repression (PTGS)	Response to stress and pathogen (bacterial) infection	Borsani et al. 2005; Katiyar-Agarwal et al. 2006; Wu et al. 2012; Zhang et al. 2012
vi-siRNA	19–25	viral genomic RNA or transcripts	TGS or PTGS	Response to virus infection	Molnár et al. 2005; Ruiz-Ferrer and Voimnet 2009
miRNA	21–22	miRNA genes producing hairpin precursors	mRNA cleavage or translation repression	Regulation of growth, development and response to stress	Guleria et al. 2011; Xie et al. 2015; Zhang and Wang 2015; Li and Zhang 2016

and processed into vi-siRNAs by the DCLs for cleaving and inactivating the viral transcripts (Ramesh et al. 2017; Paudel and Sanfaçon 2018; Guo et al. 2019). There are numerous reports to support that dsRNA treatment leads to the protection of plants against viral infection.

Studies using model plant *Arabidopsis* have shown the induction of PTI response during virus infection (Yang et al. 2010; Zorzatto et al. 2015; Niehl et al. 2016). This pathway involves the receptor kinases like BAK1/SERK3 (Somatic embryogenesis like kinase 3), BKK1/SERK4 and NIK1 (nuclear shuttle protein [NSP] interacting kinase 1), which have capability to form ligand-induced complexes with PRRs and play a central role in PTI (Brustolini et al. 2015; Niehl et al. 2016). The *Arabidopsis bak1/serk3* mutants show susceptibility towards different RNA viruses (Kørner et al. 2013) and are impaired in ethylene production (Niehl et al. 2016). This response was independent of viral dsRNA recognition by DCL (Niehl et al. 2016), as it was observed to be elicited in mutants of *dcl1* (Vazquez et al. 2006); *dcl3* (Xie et al. 2004; Henderson et al. 2006), *dcl2* and *dcl4* (Deleris et al. 2006; Garcia-Ruiz et al. 2010). The PTI signalling in response to dsRNA also involves the generation of ROS (Lee et al. 2017), induction of defense hormones and the induction of defence gene expression (Zvereva et al. 2016; Nicaise and Candresse 2017) as seen in case of peptidal PAMPs.

Viral dsRNAs are also capable of triggering the MAPK cascade to activate MPK3 and MPK6. The kinases phosphorylate eIF2- α to trigger the formation of stress granules (stored preassembled ribosome preinitiation complex) and halt translation (Makinen et al. 2017). Infection with begomovirus was shown to trigger the activation of another SERK related RPK, called NIK1 (Nuclear shuttle protein interacting kinases 1), which leads to the suppression of translational machinery (Zorzatto et al. 2015). This phenomenon was counteracted by NSP, a virus encoded virulence factor, which binds with NIK1 to allow single strand viral DNA into cytoplasm (Zorzatto et al. 2015; Gouveia et al. 2017; Calil and Fontes 2017).

The various proteins participating in small RNA biogenesis and function serve as nodes for the crosstalk with innate immunity signals. RDR1, which is involved in production of secondary vi-siRNAs is induced by SA (Wang et al. 2010), thus implicating its role in the crosstalk. Recently it was shown that DCLs share sequence homology with dsRNA helicases of RIG1 family that act as PRRs in animal systems (Fatyol et al. 2020). It was also shown that DRB4 (dsRNA binding protein 4) interacts with R-proteins to stabilize ETI, in case of *Turnip crinkle virus* (TCV) infection (Zhu et al. 2013). DRB is an essential component of the RNA silencing machinery that supports the DCL mediated dicing activity. This observation indicated the existence of crosstalk between RNA silencing and R gene pathway. Recently,

DRB2 was recognized as a viral invasion sensor molecule during studies on *Potato Virus X* (PVX) elicited systemic necrosis in *Nicotiana benthamiana*. (Fatyol et al. 2020). Down regulation of DRB2 rescued virus mediated induction of systemic necrosis, indicating its involvement in virus induced PTI.

It was proposed that two different types of DRBs are expended to select whether the induced immune response will initiate RNA silencing or PTI (Fatyol et al. 2020). An initial response to production of viral dsRNA activates DRB4, which is associated with the RNA silencing pathway as a default process. If RNA silencing fails or gets compromised and there is accumulation of viral dsRNA in the cell, then DRB2 is activated. This observation was supported by accumulation of dsRNA and their interaction with DRB2 in *ago2* mutants. DRB2 plays an important role in switching on the PTI response and promoting systemic necrosis of infected tissue (Fatyol et al. 2020).

Virus encoded suppressors as effectors of silencing

The virus encoded RNA silencing suppressors (vRSS) serve as counter measures to the defense system of plants (Burguán and Havelda 2011; Csorba et al. 2015), suggesting the co-evolution of host and viruses. The vRSS activity is acquired as a secondary function by ordinary viral proteins required for replication and spread like coat protein (CP), movement protein (MP) or proteases. Therefore vRSS show huge diversity in their function, structure, sequence and mode of action (Bivalkar-Mehla et al. 2011; Zhao et al. 2016; Sanan-Mishra et al. 2017). The vRSS can interfere with the host silencing pathway at multiple points to block biogenesis or function of the small RNAs (Karjee et al. 2010; Kumar et al. 2014). The common sites of action are listed in Table 4. For example V2 protein of *Tomato yellow leaf curl virus* (ToYLCV) binds to SGS3 (a cofactor of RDR6), which leads to the inhibition in dsRNA generation (Glick et al. 2008). *Cucumber mosaic virus* (CuMV) 2b protein interacts with the PAZ domain of AGO1 to inhibit the RISC activity (Duan et al. 2012) and hence small RNA function.

The vRSS synergistically influence plant responses to multiple pathogens. It has been shown that co-infection of two or more related or unrelated viruses in the same plant results in severe symptom development. The classical example is provided by synergism between PVX and the potyvirus, *potato virus Y* (PVY). The expression of the PVY encoded vRSS, Hc-Pro, resulted in hyper accumulation of PVX (Pruss et al. 1997). The infection with another potyvirus, *Turnip mosaic virus* (TuMV), encoded Hc-Pro also allowed 'nonhost' bacterial pathogens to grow on *Arabidopsis* (Navarro et al. 2008). This phenomenon mainly resulted from weakening of the host defence due to suppression of the RNA silencing pathway at multiple steps (Pruss et al.

Table 4 The common sites of action by which the virus encoded RNA silencing suppressors interfere with the host silencing pathway

S.No	Mode of action	Interference effect	Viral encoded RSS proteins	Reference
1	Binding to long dsRNA	Blocks DCL action thereby preventing formation of siRNA	P22 of <i>Crini virus</i> NSS of <i>Tospo virus</i> HC-Pro of <i>Poty virus</i> P14 of <i>Aureus virus</i> P21 of <i>Clostero virus</i>	Mérai et al. 2006; Shen et al. 2010; de Ronde et al. 2014b; Landeo-Ríos et al. 2016
2	Binding to small RNA duplex	Blocks RISC function	CP, P38, P37 of <i>Carmo virus</i> P19 of <i>Tombus virus</i> P21 of <i>Clostero virus</i> p15 of <i>Peclu virus</i> HC-Pro of <i>Poty virus</i> 2b of <i>Cucumo virus</i> PNS10 of <i>Phytoreo virus</i> NSS of <i>Tospo virus</i>	Lakatos et al. 2006; Mérai et al. 2006; Du et al. 2014; Varallyay et al. 2014
3	Size independent binding to dsRNA	Blocks small RNA generation	P38 of <i>Carmo virus</i> P14 of <i>Aureus virus</i> , NS3 of <i>Tenui virus</i> P21 of <i>Beet yellow virus</i>	Mérai et al. 2006; Shen et al. 2010
4	Interaction with DCL	Inhibit dicing activity	P38 of <i>Carmo virus</i>	Deleris et al. 2006; Garcia-Ruiz et al. 2010
5	Inhibition of host small RNA biogenesis	Blocks activity of proteins like DRB4, RDR6, HEN1 etc	P6 of <i>Cucumo virus</i> HC-Pro of <i>Poty virus</i>	Glick et al 2008; Jamous et al. 2011; Zhang et al. 2012;
6	Binding to AGO or other components of RISC	Inhibits PTGS by interfering with transcript cleavage or translational repression Inhibits TGS	2b of <i>Cucumo virus</i> AC2 (C2) and AL2 (L2) of <i>Gemini virus</i> P38 of <i>Carmo virus</i> P1of <i>Ipomo virus</i> P25 of <i>Potex virus</i> P0 of <i>Polero virus</i>	Buchmann et al. 2009; Giner et al. 2010; Hendelman et al. 2013; Zhang et al. 2011a, b; Azevedo et al. 2010
7	Interaction with RDR6	Inhibits amplification of silencing and transitive siRNA biogenesis	AC2 of <i>Gemini virus</i>	Garcia-Ruiz et al. 2010; Li et al. 2014
8	Interference with TGS	Suppresses RdDM	2b of <i>Cucumo virus</i> (Shan Dong isolate of CMV)	Duan et al. 2012
9		Reduces production of the methyl donor (SAM)	AC2 (C2), of <i>Begomo virus</i> and <i>Curto virus</i>	Trinks et al. 2005; Buchmann et al. 2009; Zhang et al. 2011a, b
10		inhibiting transcription of histone methyl transferase	AC2 of <i>Begomo virus</i>	Sun et al. 2015
11	Interference with host miRNAs	Targeting AGO1	P1 of <i>Ipomo virus</i> P38 of <i>Carmo virus</i> P0 of <i>Polero virus</i> CP of <i>Nepo virus</i> P19 of <i>Yombus virus</i>	Kasschau et al. 2003; Bortolamiol et al. 2007; Rawlings et al. 2011; Karran and Sanfacon 2014 Csorba et al. 2015
12		Increasing expression of miR168, which targets AGO1	P19 of <i>Tombus virus</i> 2b of <i>Cucumo virus</i> P122 of <i>Tobamo virus</i> P38 of <i>Carmo virus</i> HC-Pro of <i>Poty virus</i>	Rawlings et al. 2011; Várallyay and Havelda 2013

2004). It was reported that vRSS activity of Hc-Pro of PVY and CP of TCV required the ethylene-inducible transcription factor, RAV2, which normally induces expression of defense genes (Endres et al. 2010). Hc-Pro-transgenic tobacco plants exhibited enhanced resistance to nonviral pathogens and *N*-mediated resistance to TMV (Nakahara et al. 2012). Another study showed that Hc-Pro interacted

with the plant calmodulin-like protein, rgs-CaM and this interaction resulted in Hc-Pro degradation by autophagy. The expression of rgs-CaM is induced after infection with different RNA viruses and it interacts with several other vRSS as well (Pruss et al. 2004).

Virus infection in plants also triggered the R-Avr interactions. Several R proteins like- Rx1/2 (against PVX coat

protein), HRT (against TCV coat protein), RCY1 (against CuMV coat protein), Sw-5 (against *Tomato spotted wilt virus* replicase protein) have been identified (Whitham et al. 1994; Cooley et al. 2000; Takahashi et al. 2001). The movement and replicase proteins of viruses are known to act as Avr factors (Moon and Park 2016). The *Cauliflower mosaic virus* (CaMV) transactivator (TAV) shows vRSS activity. It interacts with several host proteins that participate in TAV-mediated translation regulation, including TOR (target-of-rapamycin) kinase (Yu et al. 2003). TOR is a negative regulator of autophagy and normally it is inactivated in response to pathogen invasion to promote cell death. TOR-deficient plants are resistant to CaMV, but TAV binding activates TOR to block PCD (Yu et al. 2003).

Similarly, the CC-NB-LRR protein, CYR1 was implicated in resistance to *Mungbean yellow mosaic India virus* (Maiti et al. 2011). TMV and *Tomato mosaic virus*, encoded vRSS, p126 was recognized by the N and TM-2 proteins in tobacco and tomato plants, respectively. The activated N protein was re-localized to the nucleus to trigger PCD (Caplan et al. 2008). The vRSS are recognized by the R proteins to elicit the ETI response. The interactions between host plant

and invading virus are continuously evolving. Viruses normally encode a few Avr factors and play around by altering their amino acid sequences without disturbing the structure. Thus, individual strains are able to escape from the recognition resulting in occurrence of disease (Zhu et al. 2013).

Role of host miRNAs

A role for host miRNAs has also been implicated in modulating the PTI and ETI pathways. The vRSS can affect the host miRNA biogenesis and function due to the high overlap and redundancy in the RNA silencing machinery. The plants effectively use this mechanism to their advantage (Fig. 1). It has been shown that repression of miR398 positively regulates PTI and callose deposition (Li et al. 2010). The NBS-LRR genes are regulated by a variety of miRNAs like miR482 binds to the P-loop-NBS-LRR transcripts leading to simultaneous silencing of R-genes (Zhai et al. 2011), while miR472 regulated the coiled-coil-NBS-LRR transcripts (Boccaro et al. 2015). The down regulation of these miRNAs during virus invasion activates the NBS-LRR receptors to trigger PTI. The miRNA160a positively modulates

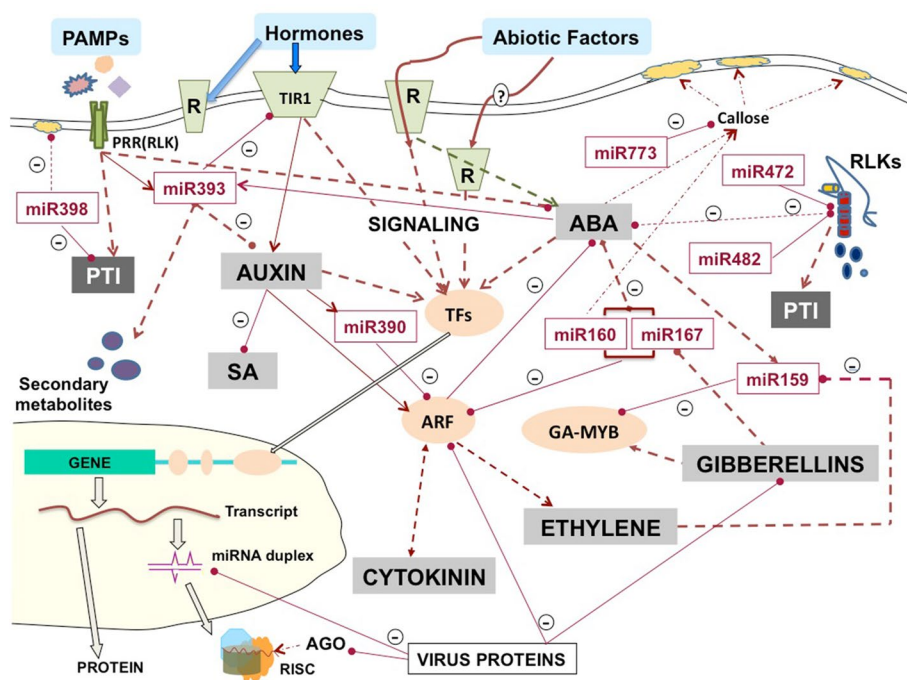


Fig. 1 Plant immunity is modulated by crosstalk between various cellular components and is regulated through key miRNA and transcription factor nodes. Different receptors (R) like PRRs, or TIR present in the cell membrane and/or cytoplasm help to perceive the biotic, abiotic and hormonal cues from the environment. Recognition of PAMPs by PRRs or RLKs leads to the activation of PTI and ETI pathways. The cellular signals converge on transcription factors (TFs), which in turn regulate the expression of genes coding for various proteins and miRNAs. The NBS-LRR RLKs are negatively regulated by miR472

and miR482. The activation of RLKs triggers a signalling cascade that leads to accumulation of miR393, which interferes with auxin production and its further crosstalk with cytokinin, abscisic acid (ABA), ethylene and Salicylic acid (SA). The hormone signals also influence expression of miRNAs like miR390, miR160, miR167 and miR159 to form complex regulatory loops to control transcription factors and gene expression. Callose deposition is an important consequence of the PTI response and it is positively regulated by miR160 and negatively regulated by miR398 and miR773

callose deposition and it has been shown that the overexpression of miRNA160a in rice, leads to higher accumulation of H₂O₂ at infection site (Li et al. 2014). There are reports on the operation of similar (miRNA regulated) mechanisms from other organisms as well. The recognition of a bacterial PAMP, flagellin leads to accumulation of miR393, which represses the auxin receptor, AFB resulting in suppression of auxin signalling to enhance plant defense (Navarro et al. 2006). It was also shown that constitutive expression of AFB1 resulted in rapid infection (Navarro et al. 2006). The passenger or star strand of miR393b was shown to control exocytosis of SA-induced PR1 and to redirect the production of secondary metabolites (Zhang et al. 2011a, b). *Blumera graminis* invasion triggered the production of miR167, miR171, miR408, miR444 and miR138, which are involved in PTI response (Gupta et al. 2012).

Relationship between virus and abiotic stress conditions

Plants are often exposed to multiple environmental factors like even a combination of abiotic and biotic stresses. Several studies have revealed synergism or antagonism between different stress factors indicating the existence of extensive crosstalk between plant responses. The level of virus pathogenicity is positively impacted by variation in the abiotic conditions which enhance plant susceptibility to biotic stresses (Wang et al. 2009; Prasch and Sonnewald 2013; Kissoudis et al. 2016; Sewelam et al. 2016; Kumar et al. 2020). Moreover, reports show that viruses upon infection can also improve the abiotic stress tolerance in plants (Xu et al. 2008; Gorovits et al. 2019; Sinha et al. 2021). Virus infection causes substantial physiological changes in their plant hosts such as reduced stomatal opening, lower transpiration rates and alterations in synthesis and translocation of metabolites (Keller et al. 1989; Matthews and Hull 2002). The lowering of stomatal conductance and transpiration lead to increase in leaf temperatures to minimize the water loss (Woo et al. 2008). The improved water retention seems to mimic the plant responses elicited by abiotic stresses such as drought, salinity and other osmotic stresses.

High temperature stress

High temperatures can significantly affect plant–pathogen interactions, as they are congenial for insect populations that carry with them payloads of pathogenic viruses. Moreover, under high temperatures the host defense responses like RNA silencing are suppressed, which increases plant susceptibility to pathogen infection (Travella et al. 2006; Prasch and Sonnewald 2013). The combination of high temperatures and drought significantly increased the susceptibility of

Arabidopsis to TuMV by suppressing the expression of PR and R genes (Prasch and Sonnewald 2013). During *Tobacco mosaic virus* (TMV) infection, it was shown that under high temperatures there was conformational change in the NB-LRR (N) protein, which perceived the TMV signal. As a result the signal transduction chain that triggered PCD, to restrict virus replication and spread, could not be initiated. Heat-dependent suppression of the HR response and R-gene mediated plant defense responses were also observed during TMV infection in tobacco and *Tomato Spotted Wilt Virus* (TSWV) infection in tomato (Zhu et al. 2010; Prasch and Sonnewald 2013).

In many cases, abiotic stress has been reported to enhance disease resistance, like heat-induced suppression of replication of *Tomato Bushy Stunt Virus* (TBSV) in tobacco protoplasts (Jones and Jackson 1990). Therefore, as a counter strategy, certain viral and fungal endophytes confer heat tolerance to the host plant (Márquez et al. 2007).

Generally, pathogenic infections have been found to weaken plant tolerance to abiotic stress. For instance, tomato plants infected with ToYLCV were more susceptible to high temperatures (Anfoka et al. 2016). This increased heat susceptibility has been associated with a down regulation of HSFs and HSPs. However, the mutualistic relationship is best exemplified by high temperature stress tolerance observed in Pigeonpea plants infected with *Pigeonpea sterility mosaic virus* (PPSMV)-I and -II (Kumar et al. 2017). Similarly, in tomato heat stress responses were induced by ToYLCV infection (Gorovits et al. 2019). It was also reported that CuMV infection enhanced cold tolerance in *B. vulgaris* (Xu et al. 2008).

Drought stress

Virus infected plants show differential responses to water deficit conditions (Bergès et al. 2018). In several cases infection with viruses like CuMV, TMV, Tobacco rattle virus (TRV) or *Brome mosaic virus* (BMV) caused accumulation of antioxidants and osmoprotectants in host plants (*Cucurbita pepo*, *Nicotiana tabacum* and *N. benthamiana*, *Solanum lycopersicum*, *Beta vulgaris*) which delayed the onset of drought symptoms (Xu et al. 2008). Similar observations were reported from wheat plants infected with *Barley yellow dwarf virus* (BYDV) (Davis et al. 2015).

Generally, viruses induce stomatal closure that have been shown to enhance drought tolerance via Abscisic acid (ABA) or SA mediated pathways (Westwood et al. 2013). It was reported that transgenic Arabidopsis plants expressing 2b protein of CuMV showed increased drought tolerance via ABA-mediated signalling pathway (Westwood et al. 2013). The virus infection resulted in altered morphology of the roots and decreased stomatal permeability and water loss thereby stimulating drought tolerance

(Westwood et al. 2013). Similarly *Rice tungro spherical virus* (RTSV) infected rice plants showed a delayed response to drought stress due to increased leaf hydration, less negative leaf water potential and enhanced stomatal conductance (Grimmer et al. 2012; Encabo et al. 2020). The C4 protein encoded by ToYLCV enhanced drought tolerance in *Nicotiana benthamiana* and tomato through an ABA-independent mechanism (Corrales-Gutierrez et al. 2020).

Salt stress

Salinity stress constitutes one of the major abiotic stress, which creates adverse conditions for plant growth and seed germination. High salt concentration in soil causes ionic and osmotic stress resulting in cellular damage, reduction in turgor pressure and subsequently stomatal closure (Miller et al. 2010). It was shown that salinity stress favoured spread of bacterial and viral pathogens within plants to enhance infection (Kissoudis et al. 2016; Varela et al. 2019). Cowpea plants become more susceptible to *Cowpea severe mosaic virus* (CpSMV) infection when exposed to salinity stress (200 mM NaCl) either simultaneously or 24 h prior to CPSMV inoculation (Varela et al. 2019). Similarly, it was reported that *Nicotiana benthamiana* plants subjected to osmotic, salt and wounding stresses became more susceptible to *Potato virus A* (Suntio and Mäkinen 2012). Studies in our lab have shown that overexpression of insect *Flock House Virus* B2 protein, in tobacco and rice enhances tolerance to salt stress by increasing stomatal conductance, photosynthetic efficiency and proline accumulation (Sinha et al. 2021).

Molecular mechanisms of crosstalk

Pathogenic plant viruses are parasitic symbionts as they depend on host resources for their reproduction, transmission and infection (Islam et al. 2017; Takahashi et al. 2019). During this process, they exert a strong influence on the vegetative and reproductive performance of plants by directly or indirectly stimulating the defense responses, disrupting the phytohormone accumulation and signals and altering the expression of transcription factors (Ma and Ma 2016). The main modes of crosstalk include the recognition by generic set of receptors to generate signalling cascades that culminate on transcription factors to alter gene expression. During this process the phytohormone profiles are also modulated and they respond antagonistically or synergistically to regulate response to stresses (Checker et al. 2018).

Receptors

The PRRs comprise a diverse family of cell surface-localized receptors (Frescatada-Rosa et al. 2015), including the RLKs and RPKs (Goff et al. 2007). RLKs belong to a gene superfamily, which contains 610 and 1131 members in *Arabidopsis* and rice, respectively (Gish and Clark 2011). They are classified into 44 subfamilies including LRRs, lectins, epidermal growth factor-like repeats, lysine motifs, self-compatibility domain and wall associated kinase (Frescatada-Rosa et al. 2015). The LRRs are known play essential roles in regulating growth and development, grain yield, hormone perception, initiating PTI responses and adaptation to abiotic stresses (Osakabe et al. 2013; Macho and Zipfel 2014; Zou et al. 2015). The RLKs contain extracellular ligand-binding domains that can perceive a wide range of PAMPs and abiotic stresses signals (Fig. 1). The ligand binding triggers phosphorylation of their intracellular serine/threonine kinase domains to activate downstream intracellular signalling cascades (Zipfel 2014; Trdá et al. 2015). In *Arabidopsis* a cytosolic cysteine-rich RLK, ARCK1, negatively regulates ABA and osmotic stress signal transduction (Tanaka et al. 2012). When the kinase activity is inactivated by mutation the plants show higher sensitivity to ABA and osmotic stress. CRK36, is another member of the RLK family that interacts with ARCK1 to fine-tune plant responses to abiotic stresses via hormone signalling (Tanaka et al. 2012). Studies also showed the involvement of GbRLK in response to both biotic and abiotic stresses. It mediated the reduction in rate of water loss and increased sensitivity to ABA to confer tolerance to salinity and drought stress and resistance to Verticillium wilt in transgenic cotton and *Arabidopsis* lines (Zhao et al. 2013; Jun et al. 2015).

Phytohormones

Phytohormones like Auxin, Cytokinins (CKs), Gibberellins (GA), ABA and Ethylene (ET) are involved in regulating various aspects of plant growth, development, reproduction and defense in response to virus infection (Adie et al. 2007; Tamaoki et al. 2013). Thus, extensive crosstalk and interactions operate between the diverse phytohormonal pathways to regulate plant physiology in response to virus attack (Pacifi et al. 2015). Role for several vRSS has been implicated in the development of disease symptoms by altering the hormone signals (Wang et al. 2012). *Arabidopsis* plants ectopically expressing TuMV silencing suppressor HC-Pro or *Beat curly type virus* (BCTV) encoded C4 protein show developmental leaf abnormalities as seen during virus infection (Kasschau et al. 2003; Mills-Lujan and Deom 2010). The vRSS, P6, encoded by CaMV when over-expressed in *Arabidopsis* plants resulted in stunting, chlorosis and

banding of vein in leaves by interrupting multiple hormonal pathways (Rodriguez et al. 2014).

The ABA, ET, SA and JA comprise core group of defense-related phytohormones that are produced in response to both, biotic and abiotic stresses (Kissoudis et al. 2016; Schwessinger et al. 2015). Biotic stress and the resistance inducing compounds, also trigger primed state of defense. In *Arabidopsis* plants primed by BABA (beta-aminobutyric acid) or inoculation of an avirulent *Pseudomonas syringae* strain PstavrRpt2, the progeny showed higher accumulation of defense related transcripts. This also made the progeny plants more resistant to the virulent pathogens. If additional priming treatment, was provided to the already primed progenies they exhibited much stronger defense response (Slaughter et al. 2012). Chromatin immunoprecipitation analysis revealed the involvement of epigenetic regulation in this process. H3K9 acetylation of SA inducible promoters lead to permissive transcription while methylation at H3K27 of JA inducible promoters lead to repression of JA marker genes like PDF1.2. It is hypothesized that trans-generational SAR is transmitted by hypomethylated genes to direct the priming of SA dependent defenses in subsequent generations (Luna et al. 2012).

Auxin, gibberellin and cytokinin

Auxin is the most important phytohormone that regulates different aspects of plant growth and development. GA is also considered a major plant growth hormone known to stimulate stem elongation, flowering and germination. The CKs are tightly linked to auxin in promoting lateral organ development. Auxin and CK act in an antagonistic manner to regulate cell division and differentiation. Auxin supports cell division and maintenance of the apical meristem while CK promotes cell differentiation by repressing the polar auxin transport. It has been reported that SHY2 acts as a central molecule to negatively regulate Aux/IAA signalling (Calderson Villalobos et al. 2012). Its expression is induced by CK but the protein is degraded by auxin (Ioio et al. 2008). GA also participates in SHY2 regulation by repressing the CK-dependent transcriptional activation of SHY2 (Moubayidin et al. 2010).

Symptoms generated during virus infection resemble the phenotypic disorders seen in plant mutants having disrupted hormone signalling like leaf curling, stunting, mosaic and mottle or gibberellin deficiency like leaf darkening and stunting (Schaller et al. 2015). It has been shown that auxin and GA functions are directly interrupted by viral components (Jin et al. 2016). The replication proteins of TMV interact with the Aux/IAA family members to disrupt the signalling pathway, which results in development of disease symptoms such as leaf curling (Collum et al. 2016). The interference with phloem specific Aux/IAA prevents

their translocation to the nucleus resulting in inhibition of the Auxin responsive TFs (ARFs). This reduces the auxin levels in the phloem and facilitates enhanced virus loading and their systemic movement (Collum et al. 2016). Similarly *Rice dwarf virus* (RDV) also induces symptoms like stunting in the infected rice plants, which can be recued by exogenous application of GA (Zhu et al. 2005). It was reported that the symptoms appear due to direct interaction between the RDV-P2, an outer capsid protein and the rice IAA10 and *entkaurene oxidase*, a key enzyme in GA biosynthesis (Hayashi et al. 2010; Satoh et al. 2011). P7-2 capsid protein encoded by *Rice black streaked dwarf virus* (RBSDV) interacts with GID2 (Gibberellin Insensitive Dwarf 2) to lower the levels of GA (Huang et al. 2017). GA can modulate the levels of SA and JA/ET depending upon the biotrophic or necrotrophic nature of infection (Robert-Seilaniantz et al. 2007). The CKs also work synergistically with SA to stimulate defense responses, through activation of *Arabidopsis* response regulators (ARRs) The ARR can bind to promoters to induce the expression of genes, such as PR1, PR2, PR5, SID1 and SID2 which are involved in plant defense and SA biosynthesis (Choi et al. 2010). The exogenous application of CK, dihydrozeatin was shown to reduce accumulation of *White clover mosaic potexvirus* (WCMV).

Ethylene, salicylic acid and jasmonic acid

Ethylene (ET) is a pleiotropic hormone, which promotes fruit ripening and organ senescence. It is also involved in plant defense (Graham et al. 2011; Pieterse et al. 2012). Mutants of ET biosynthesis such as *acs1*, *ein2* and *erf106* were resistant to TMV-cg infection, but exogenous application of ACC increased the susceptibility of treated plants. TMV infection in *Nicotiana tabacum*, lead to the formation of lesions where ACC and/or ET accumulated. However, if ACC was sprayed before the infection, it prevented the formation of necrotic areas (de Laat and van Loon 1983; Ohtsubo et al. 1999; Alazem and Lin 2015; Lovato et al. 2019). In *Phaseolus vulgaris* the application of ACC reduced the virus (WCIMV) titres (Clarke et al. 1999). The ET pathways show synergistic interaction with ABA. During CMV infection, the levels of ABA and ET were increased and this resulted in suppression of hypocotyl elongation (Aharoni et al. 1977).

Salicylic acid (SA) and Jasmonic acid (JA) are majorly responsible for the plant's reaction to biotic stresses. SA is the main phytohormone responsible for induction of SAR, which is considered as a type of long lasting immune memory. Antagonistic relationship has been observed for SA- and JA/ET-mediated defense pathways during virus infection. Exogenous application of methyl jasmonate to TMV resistant tobacco decreases resistance and facilitates systemic movement of virus (Robert-Seilaniantz et al. 2011).

Depletion of endogenous SA- or disruption of SA-signalling pathway leads to the impairment of defense response and susceptibility to viral infection (Yang et al. 2015).

SA acts through NPR1 (Nonexpressor of PR genes 1), which is the key regulator of transcriptional reprogramming (a primed memory) during SAR. It has been hypothesized that in healthy tissue, when there is no accumulation of SA and NPR1 exists as an inactive oligomer bound to NPR4/NPR3 and is degraded by 26 proteasome complex. Upon infection, the gradual elevation of SA alters the cellular redox potential and this causes release of NPR1 due to reduction of its disulfide bonds. The NPR1 monomers are post-translationally modified in the presence of SA and are targeted to the nucleus, where they interact with TGA transcription factors to induce PR gene expression. The SA primed removal of NPR1 also elicits necrosis as NPR1 acts as a negative regulator of PCD (Fu et al. 2012). The *npr1* mutants are susceptible to diseases due to failed SAR while the over expression of NPR1 gives broad spectrum resistance. Accumulation of SA decreases salicylate hydrolase by the use of NahG transgene that negates resistance provided by the potato Ny-1 R-gene against *Potato virus Y* (Baebler et al. 2014). Viral proteins like CaMV encoded P6 protein and TMV replication protein inhibit SA-dependent defense response by causing mis-localization of the inactive form of NPR1 to the nucleus thereby disrupting the SA-signalling pathway and making the plants more susceptible to pathogens (Love et al. 2012; Wang et al. 2012). In *Arabidopsis thaliana*, TMV-Cg coat protein (CgCP) was shown to suppress SA-signalling pathway by stabilizing DELLA proteins that negatively regulate and represses SA-mediated defense response, thus acting antagonistically between SA and JA pathways (Rodriguez et al. 2014).

The activation of PTI pathways also triggers JA mediated defense response (Shi et al. 2019). Activation of JA depends on regulation of a F-box protein, COI1 (Coronatine insensitive 1). JA acts as the mobile signal through MYC and ERF (Ethylene response factor) pathways to trigger biosynthesis of various chemicals to counter pathogen invasion (Berrocal-lobo et al. 2002; Kazan 2015). The ERF-TF branch in JA pathway is cross-influenced by ET and SA signals. It has been observed that at low concentrations the SA and JA show synergistic effects on expression of defense marker genes, but at higher concentrations their effect is antagonistic (Mur et al. 2006). The JA signals also inhibit DELLA repressor IAA59 and HY5 to interfere with the GA, auxin and light signalling pathways (Hou et al. 2016).

The JAZ–MYC complex comprises another main branch of the JA signalling pathway. In healthy tissues, when JA levels are low, JAZ is expressed which acts as a repressor of defense genes by binding to MYC2 (Pavwels et al. 2010). In presence of JA, MYC2 is released from the JAZ repressor complex to activate defense related genes

and SA production. It has been shown that foliar spray of meJA reduced RBSDV infection in rice (He et al. 2020). The JAZ–MYC complex is one of the common targets of plant viruses to suppress plant defenses. The β -C1 protein produced by begomovirus satellites and ToYLCV encoded proteins interact with MYC2 (Li et al. 2019) while 2b protein of CuMV interacts with JAZ to suppress the activity of defense genes (Wu et al. 2017). The β -C1 also controls WRKY20, which are expressed in phloem to control SA induced immunity (Zhao et al. 2019a, b), as SA receptors, NPR3 and NPR4, show positive effects on JA signalling by inhibiting JAZ receptors (Liu et al. 2016).

Abscisic acid

ABA is predominantly involved in abiotic stress adaptation, but it acts as a negative regulator of pathogen resistance by inhibiting SA, JA and ethylene activated transcription of plant genes required for pathogen resistance. The ABA responses are manifested through Ca^{2+} gradients and MAPK cascades coupled to ROS signals to form flexible feedback loops. The first response of ABA during both biotic and abiotic stress is stomatal closure allowing reduction in water loss and maintaining beneficial water potential. As a secondary response, ABA signals induce callose deposition at the site of pathogen invasion, by inhibiting the activity of callose degrading enzyme, β -1,3 glucanase (Mauch-Mani and Mauch 2005). It has been elucidated that ABA and ROS can function in a positive amplification loop to control stomatal function and gene expression. ABA also acts by regulating the RNA silencing machinery. The *dcl-11*, *hen1*, *dcl2*, *dcl3* and *dcl4* mutants showed hypersensitivity towards ABA while *aba1-5* mutants showed increased concentration of AGO1 (Li et al. 2013a, b). Moreover, ABA responsive elements (ARE) are present in their promoter region of miR168a, which targets the AGO1 (Li et al. 2013a, b).

It was shown that exogenous application of ABA or drought stress increased the susceptibility of plants to several *Pseudomonas syringae* and other bacterial strains (Fan et al. 2011). This effect was mediated *Nine cis-Epoxy-carotenoid Dioxygenase 5* (NCED5). The overexpression of NCED5 lead to a > twofold increase in ABA content, which increased the pathogen susceptibility (Jiang et al. 2010; Fan et al. 2011; Choi et al. 2013). During invasion by TMV and *Bamboo mosaic virus* (BaMV), ABA and SA are induced simultaneously (Alazem and Lin 2015) to increase plant resistance, but actually, ABA shows strong antagonism with SA. ABA mutants, *nced3* and *aba2-1* show reduced titres of BaMV and CMV (Alazem and Lin 2015).

Transcription factors

The response to biotic and abiotic stimuli involves massive transcriptional reprogramming that is intricately coordinated through the various signalling cascades that converge on the transcription factors (TFs) like MYBs, NAC, AP2 and so on. Most of these TFs also serve as critical miRNA-regulated nodes in phytohormone pathways thus facilitating cross regulations (Fig. 1).

The Auxin responsive ARFs have antiviral functions and they primarily act by targeting the viral proteins to SCF complex for proteasomal degradation (Qin et al. 2020). The vRSS like Hc-Pro, P19 and P15 deregulate miR167 to enhance suppression of ARFs (Jay et al. 2011). During PVY infection, the levels of GA are lowered to cause accumulation of miR167 to enhance suppression of ARFs (Kriznik et al. 2017).

The MYB-TF encoding *botrytis susceptible 1 (bos1)* gene was shown to confer resistance to pathogens and tolerance to salt, drought and oxidative stresses by regulating the JA and GA signalling pathways (Mengiste et al. 2003).

The NACs represent a large plant-specific family of TFs that play a crucial role in plant development and response to stress (Hernandez and Sanan-Mishra 2017). One of the NAC member, *Arabidopsis thaliana* activating factor1 (ATAF1) is a stimulus-dependent regulator of ABA biosynthesis. Its expression is induced in response to salinity and drought stress in an ABA-independent manner (Lu et al. 2007; Wu et al. 2009). ATAF1 knockout mutants have high levels of several stress responsive genes such as COR47, ERD10, KIN1, RD22 and RD29A (Lu et al. 2007; Wu et al. 2009) and pathogenesis related (PR) genes, PR-1 and PR-5 (Lu et al. 2007). Therefore, ATAF1 acts as a critical node in regulating the antagonistic interplay between ABA- and JA or ET-signaling pathways. It was also shown that ATAF1 acts as an activator of senescence-promoting TF, ORESARA1 (AtNAC092) and repressor of MYB-TF GOLDEN2-LIKE1 (Garapati et al. 2015). Similarly, OsNAC6, which shows high similarity to genes in the ATAF subfamily, was shown to be a positive regulator of plant response to biotic and abiotic stresses (Nakashima et al. 2007). TMV replication protein targets degradation of ATAF2 to regulate basal defense responses (Wang et al. 2009). Expression of OsNAC6 was induced by cold, drought, high salinity, wounding, ABA, JA and blast disease in rice (Ohnishi et al. 2005; Nakashima et al. 2007; Takasaki et al. 2010). The expression of OsNAC5 was induced under drought, cold, high salinity, ABA and methyl-JA to increase the expression of stress-responsive genes, such as OsLEA3 (Takasaki et al. 2010).

The heat shock TFs (HSFs) also play a central role in response to multiple abiotic and biotic stresses via ABA-dependent signalling pathways (Chung et al. 2013; Xue

et al. 2015). Scientific evidence suggested that HSFA2 and HSFA4A are responsive to oxidative stress signals during heat and pathogen attack (Scarpeci et al. 2008). In Arabidopsis, AtHsfA6a transcript was induced under high salinity and dehydration conditions (Hwang et al. 2014). HsfA3 was associated with response to drought and salt stress (Li et al. 2013a, b), while HSF4 was induced by salinity and/or osmotic stress and fungal infection (Sham et al. 2015).

Summary and perspectives

Being sessile organisms, plants have evolved a plethora of complex overlapping response pathways, which enable them to survive a combination of environmental (biotic and abiotic) stresses. The different phytohormones are known to interact for coordinating plant growth in response to environmental changes. The plant immune system is activated by complex interactions between the pathogenic elicitor or effectors and host receptors molecules. Experimental evidence also highlights the presence of substantial overlap with the response to abiotic stresses, particularly heat, drought and salinity. Thus, exposure to biotic stress, like virus infection or pathogen attack can also give cross tolerance to abiotic stresses and vice versa. It is apparent that participation of ROS signals, MAP kinase cascades and phytohormones are common responses to both biotic and abiotic stresses. There is also recognition for the role of receptor proteins as key initiators of the crosstalk. The various signalling cascades converge on TFs which positively or negatively regulate gene expression to reprogramme the genetic machinery for increasing plant tolerance to subsequent spell of one or the other stress. The TF nodes are fine tuned by a variety of small RNAs that play a significant role in crosstalk. The cross interactions between TFs and small RNAs generate a series of regulatory nodes that enable plants to rapidly respond to diverse environmental challenges and coordinate these responses with developmental programs for endurance and survival. However, the complete understanding of crosstalk between the cellular components that facilitate plant survival in response to diverse stresses is still limited. In depth studies are required to identify the central hubs controlling the plant defense mechanisms and stress signalling interactions. The intricacies of interactions between the TFs and small RNAs involved in the regulation of stress- and hormone responsive genes need to be elucidated. The availability of high throughput sequencing, bioinformatics tools and advances in imaging technologies will support the genome-wide transcriptome and proteome studies to provide insights into the molecular components and pathways operating in response to a variety of stresses. Another challenge will be to dissect the common and specific pathways, with

respect to each stress condition, which prime the plants and provide a crosslink to stress adaptations. This will help in designing effective strategies to negate the effect of stresses on plant growth and productivity.

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Declarations

Conflict of interest Authors declare that they have no conflict of interest.

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