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Plant microRNAs: Front line players against invading pathogens

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ABSTRACT

Plants are attacked by a large number of pathogens. To defend against these pathogens, plants activate or repress a vast array of genes. For genetic expression and reprogramming, host endogenous small RNAs (sRNAs) are the key factors. Among these sRNAs, microRNAs (miRNAs) mediate gene regulation through RNA silencing at the post-transcriptional level and play an essential role in the defense responses to biotic and abiotic stress. In the recent years, high-throughput sequencing has enabled the researchers to uncover the role of plant miRNAs during pathogen invasion. So here we have reviewed the recent research findings illustrating the plant miRNAs active involvement in various defense processes during fungal, bacterial, viral and nematode infections. However, rapid validation of direct targets of miRNAs is the dire need of time, which can be very helpful in improving the plant resistance against various pathogenic diseases.

1. Introduction

Food security is continuously being challenged due to various virulent crop pathogens [1]. These pathogens may include fungi, bacteria, viruses, nematodes and other parasites. For defense against these pathogens plants have evolved small RNAs (sRNAs) playing an active role in managing immunity against pathogen attack [2,3]. These sRNAs are classified as small interference RNAs (siRNAs) and micro RNAs (miRNAs). Among them, the miRNAs (21 nucleotides in length) are considered more diverse, more active and are more in the attention of the researchers worldwide for enhancing crop immunity against plant pathogens [4–7]. miRNAs were first discovered in *Caenorhabditis elegans* [8]. With the passage of time, miRNAs and their roles in the plant life cycle are being described [9]. Modern bioinformatics, genetics, biochemical and molecular approaches lead the researcher to investigate regulatory functions of miRNAs in plant pathogenic interactions [10]. Next-generation sequencing methods have elaborated the miRNAs functioning through transcription, induced silence complex loading, processing, turnover and decay [11]. All of these processes are regulated by many other factors such as RNA editing, genetic mutations, complementarity, target availability and other temporal effects thus ensuring the versatility of miRNA functions and activities. miRNA undergoes RNA polymerase II-dependent transcription [12–14] followed by recognition of the single-stranded RNAs by Dicer-Like1 (DCL1) in plants [15–17]. This recognition further leads towards the conversion of the primary miRNAs (pri-miRNAs) to the precursor miRNAs (pre-miRNAs) and finally to the miRNA/miRNA* duplexes [18,19]. miRNAs are then dissociated from duplexes and are further incorporated into Argonaute (AGO)-associated miRNA-induced silencing complexes (miRISCs; preferentially AGO1-associated miRISCs) [20,21]. Regarding biogenesis of miRNAs, several studies are available [22–27]. Each step of miRNA biogenesis is influenced and surveillanced by many cis- and trans-factors. These may include chromatin marks and specific transcription factors (TFs) [28]. Although sequences and structures of miRNAs determine their integral efficiency, yet several spatiotemporal factors also regulate miRNA precursors processing in plants [29,30]. Furthermore, there is competition between miRNAs and other sRNAs for their loading into AGO complexes which sometimes results in non-uniform loading of various miRNAs into AGO1-associated miRISCs [31]. Expression of a particular gene in plants via recognition through

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transcripts is further influenced by miRNA guided miRISCs. The process is smoothly performed and involve several complementary events for ensuring the affectivity upon regulatory processes of miRNAs [32]. For instance, complementarity and target abundance determines the degradation rate of miRNAs [33–35]. Completion of one cleavage of a specified target may or may not result in the degradation of miRISC because the particular miRISC have the survival ability or regeneration ability through a released miRNA [36,37]. This survival or regeneration can lead towards another round of target cleavage. The completion speed of this particular process is dependent upon the complementarity of a target. The turnover rate is reduced for miRNAs sequestered by bulge targets [38]. All these events advocate vigorous regulatory activities of miRNAs. miRNAs are explicitly employed by plants in response to pathogenic attacks. Therefore, we have reviewed plant defense responses aided by diversified miRNAs against fungal, bacterial, viral or nematode attack. The review includes topical research analyses illustrating miRNAs as defenders against various pathogens.

2. Plant defense mechanism against pathogen attack; miRNA prospective (an overview)

Plants are the source of food and survival for all types of organisms [39–42]. Among the plant pathogens, virus, bacteria, fungi and nematodes are more prominent as they cause economically important diseases. Theses pathogens either directly destroy the plant cells by inserting their hyphae e.g., fungi or utilize host machinery for their reproduction [43,44] as well as further distribution i.e., viruses [45–51]. To defend against these pathogens, plants have evolved several mechanisms such as structural defense, chemical defense, hypersensitive response and systemic acquired resistance. One of these sophisticated mechanism involves the activation of self-defense responses through the involvement of miRNAs due to absence of some specialized plant cells with immune functions [52]. This involves the recognition of pathogen-associated molecular patterns (PAMPs), for pathogen recognition and triggering the first line of defense, i.e., primary immune defense [53]. In response, the pathogens have also developed particular effectors which suppress this first defense line of plants via interrupting the signal transition of PAMP-triggered immunity (PTI) [54]. To counter this pathogen strategy, plants have evolved the second line of defense called effector-triggered immunity (ETI) regulated via various resistance (R) proteins [55–57]. These R proteins are more precise and accurate in inhibiting the growth of the bacterial pathogen effectors, such as avirulence (avr) proteins [58–60]. In response, miRNAs are induced or repressed to modulate and regulate the gene-expression through gene silencing at transcriptional or post-transcriptional level via alteration in various hormones such as auxin, abscisic acid (ABA) and jasmonic acid (JA). Diverse miRNAs actively participate in defense against various pathogens (Table 1). The detailed response via plant miRNAs is explained as under.

3. Response of plant miRNAs to fungal infections

The modern technology has enabled researchers to explain the defensive roles of plant miRNAs against various fungal disease attacks. Yin et al. [95] identified various miRNAs endowing resistance against *Verticillium dahlia* in two cotton cultivars, i.e., Hai-7124 and Yi-11. They documented the expression profiles of 65 miRNAs which show their altered expression in response to the *Verticillium*. Among them, Ptc-miR482, Ptc-miR1444 and Ptc-miR1448 were specified to cotton cultivars which indigenously exhibited the PPO (Polyphenol oxidase) gene cleavage along with the other disease resistance-related genes for regulating biotic and abiotic stress resistance [96,97]. In fungal infected plant roots, miR482 and miR1448 were down-regulated showing increased PPO along with the disease resistance. Correspondingly [98], several miRNAs were identified from rice cultivars with differential expressions upon the infection of *Magnaporthe oryzae* under standard normal conditions. These miRNAs exhibited a negative expression of some target genes via real-time RT-PCR assay. Further analysis revealed over-expressed miR160a and miR398b along with up-regulation of defense-related genes and H_2O_2 accumulation at the infection site in transgenic rice. This significantly increased the resistance to *Magnaporthe oryzae* [98]. *Dothiorella gregaria* causes gummosis and rot in *Populus beijingensis*is. In infected Populus plants, Chen et al. [81] identified 74 conserved miRNAs along with 27 novel miRNAs from 37 different miRNA families. Further sequencing explained that out of the ten out of 74 conserved miRNAs were over-expressed while miR472, miR1447 and miR1448 targeted the disease resistance genes [99]. It was documented that the infected plants displayed enhanced production of miR1142 and miR1447 while genesis of miR472 and miR1448 was significantly reduced. Contrarily, Lu et al. [100] explained the induction of pbe-miR156a-e in *Dothiorella gregaria* infected Populus plants and repression of miR156 in *Cronartium quercuum* infected stem of loblolly pine. Recently, Salvador-Guirao et al. [101] investigated the role of miR773 in modulating resistance to infection by fungal pathogens in *A. thaliana*. They concluded that interference with miR773 activity by target mimics (in MIM773 plants) and concomitant up-regulation of the miR773 target gene *METHYLTRANSFERASE 2 (MET2)* considerably increased resistance to *Plectosphaerrella cucumerina*, *Fusarium oxysporum* and *Colletototrichum higginianum* infection. From these results, we can hypothesize that same miRNAs may show diverse functions in varying plant species under the stress of different pathogen attack (Fig. 1). Therefore, to better understand the regulatory role of miRNAs on their target genes during fungal infection, further experimental validation is indispensable.

Plant hormones also play their active role in plant immunity. It has been witnessed that the relationship between miRNAs and phytohormone responses improves understanding of miRNAs and hormone action in disease control [102,103]. First discovery regarding miRNAs (miR393) involvement in the regulation of auxin signaling pathway was discovered in anti-bacterial response of *Arabidopsis thaliana* through active contribution in PTI [104]. This laid the foundation to exploit PTI in various plants against pathogen attack through induction of miRNAs [105]. This was achieved via incorporation of avirulent pathogens in *Arabidopsis,* which resulted in hypersensitive response causing the down-regulation of miR398 during bacterial infections [70]. The same phenomenon was observed in anti-fungal infections as chitin is considered as one of the most important structural components of fungi [106,107]. Chitin triggered immunity through delivery of effectors into the plants against *Cladosporium fulvum* infections was demonstrated through the involvement of Ecp6, i.e., the LysM domain–containing effector proteins [108–110]. Fungal chitin treated tomato and tobacco mutants showed enhanced ROS (reactive oxygen species) production along with the elevated levels of Cu/Zn SOD proteins under control conditions. Increased ROS detoxification was observed due to elevated SODs. Regulation of miR398 results in reduced CSD1 and CSD2 mRNA levels thus conferring its role in fungal infections [111]. Fungal historia can also deliver effectors into plant intercellular spaces [112] but the enzymatic activity of these effectors have been demonstrated for only a few interacting miRNAs. A large number of miRNAs which play as a defender against various fungal pathogens remain still unknown.

The auxin is critically responsive towards biotic and abiotic stresses in plants. The enhanced auxin-mediated response in wheat cultivars against powdery mildew infection was observed upon the down-regulation of transport inhibitor response 1 (TIR1), i.e., a negative regulator of auxin signaling. Moreover, up-regulation of miR393 which targets the TIR1 auxin receptor was found in *Blumeria graminis* infected *Triticum aestivum*, thus initiating defense against the invading fungus [113]. Three independent responses (lignin biosynthesis, hormone signaling, and protein biosynthesis) in *Puccinia graminis* infected wheat plants were regulated via targeting various transcription factors through eight miRNAs namely miR159, miR164, miR167, miR171, miR408, miR444, miR1129 and miR1138. Among them, miR167,

Table 1
Defensive role of miRNAs against various pathogens.

miRNAs	Defensive role in plant specie	Name of Pathogen	Pathogen Type	Target gene	References
amiR159	*Arabidopsis*	TYMV	Virus	*P69, HC-Pro*	[61]
miR159a	*N. benthamiana*	PPV	Virus	*P1/HC-Pro*	[62]
miR167b	*N. benthamiana*	PPV	Virus	*P1/HC-Pro*	[62]
miR171a	*N. benthamiana*	PPV	Virus	*P1/HC-Pro*	[62]
miR393	*Arabidopsis*	*Pseudomonas syringae*	Bacteria	*TIR1*	[63]
miR825	*Arabidopsis*	*P. syringae*	Bacteria	*Remorin, zinc finger homeobox family, frataxin-related*	[64]
miR393	*Arabidopsis*	*P. syringae*	Bacteria	*AFB2, AFB3*	[64]
miR167	*Arabidopsis*	*P. syringae*	Bacteria	*ARF8*	[64]
amiR171	*N. tabacum*	CaMV	Virus	*2b*	[65]
miR1885	*Brassica napus*	TuMV	Virus	*TIR–NBS–LRR*	[66]
Pre-miR171a	*Arabidopsis*	CMV	Virus	*3′-UTR*	[67]
miR1448	*Populus trichocarpa*	*Botryosphaeria dothidea*	Fungus	*S-conjugate, ABC transporter, ATP-binding cassette transport protein*	[68]
Pre-miR159	*Arabidopsis*	TuMV	Virus	*P69*	[69]
miR398	*Arabidopsis*	*P. syringae*	Bacteria	*COX5b.1*	[70]
miR773	*Arabidopsis*	*P. syringae*	Bacteria	*MET2*	[71]
miR398	*Arabidopsis*	*P. syringae*	Bacteria	*CSD1, CSD2*	[71]
miR160	*Arabidopsis*	*P. syringae*	Bacteria	*ARF10, ARF16, ARF17*	[71]
miR159a	*N. tubacum*	PVY	Virus	*HC-Pro*	[72]
miR167b	*N. tubacum*	PVX	Virus	*TGBp1/p25*	[72]
miR171a	*N. tubacum*	PVX	Virus	*TGBp1/p25*	[72]
Pre-miR159a	*Solanum lycopersicum*	CMV	Virus	*2a, 2b*	[73]
miR159	*Arabidopsis*	*P. syringae*	Bacteria	*MYB33, MYB65, MYC101*	[73]
miR167	*Arabidopsis*	*P. syringae*	Bacteria	*ARF6*	[73]
miR408	*Arabidopsis*	*P. syringae*	Bacteria	*Copper protein plantacyanin and copper ion binding protein genes*	[73]
miR390	*Arabidopsis*	*P. syringae*	Bacteria	*TAS3*	[73]
miR393b	*Arabidopsis, N. benthamiana*	*P. syringae*	Bacteria	*MEMB12*	[74]
miR482	*Solanum lycopersicum*	TCV, CMV, TRV	Virus	*NBS-LRR*	[75]
Pre-miR159a	*N. benthamiana*	WSMoV	Virus	*L replicase gene (Conserved motifs)*	[76]
miR395	*Triticum*	WSMV	Virus	*Conserved region*	[77]
pre-miR319a	*Vitis vinifera*	GFLV	Virus	*Coat protein (CP)*	[78]
miR160	*Pinus taeda*	*Cronartium quercuum f. sp. fusiforme*	Fungus	*Auxin response factor, Aux/IAA*	[79]
miR482	*Cotton*	*V. dahliae*	Fungus	*Disease resistance protein*	[80]
miR1447	*Populus beijingensis*	*Dothiorella gregaria*	Fungus	*Disease resistance protein*	[81]
miR1448	*Cotton*	*V. dahliae*	Fungus	*Disease resistance protein,*	[80]
miR1448	*P. beijingensis*	*D. gregaria*	Fungus	*Glutathione*	[82]
miR1450	*P. trichocarpa*	*B. dothidea*	Fungus	*Leucine-rich repeat*	[82]
miR160	*P. trichocarpa*	*B. dothidea*	Fungus	*Auxin response factor, Aux/IAA*	[82]
amiR-AV1-1	*Tomato*	ToLCNDV	Virus	*AV1 and AV2*	[83]
pre-miR169a	*N. benthamiana*	CLCuBuV	Virus	*V2 gene*	[84]
pre-miR319a	*S. lycopersicum*	ToLCV	Virus	*AV1 and AV2 (coat protein)*	[83]
miR5300	*S. lycopersicum*	*F. oxysporum*	Fungus	*Solyc05g008650, tm-2*	[85]
miR472	*Arabidopsis*	*P. syringae*	Bacteria	*CC-NBS-LRR*	[86]
pre-miR319a	*N. benthamiana*	PVY	Virus	*CI, NIa, NIb, CP*	[87]
miR6019/ miR6020	*N. tabacum*	TMV	Virus	*TIR-NBS-LRR*	[88]
miR396a-5p	*Solanaceae*	*P. infestans*	Bacteria	*GRF*	[89]
pre-miR171	*N. benthamiana*	WDV	Virus	*Conserved region*	[90]
pre-miR528	*Oryza sativa*	RSV, RBSDV	Virus	*Middle segment, 30 end*	[91]
pre-miR159a	*N. benthamiana*	CBSV, UCBSV	Virus	*P1, P3, CI, Nib and CP*	[92]
pre-miR159a	*N. benthamiana*	TSWV	Virus	*N, NSs*	[93]
miR396	*Arabidopsis*	*Plectosphaerella cucumerina, Botrytis cinerea, F. oxysporum f. sp. Conglutinans, Colletotrichumhigginsianum, P. cucumerina, B. cinerea*	Fungus	*GRF*	[94]

Abbreviations for virus names include in this table are: TuMV; *Turnip mosaic virus*, TCV; *Turnip crinkle virus*, CMV; *Cucumber mosaic virus*, TRV; *Tobacco rattle virus*, RSV; *Rice stripe virus*, RDV; *Rice dwarf virus*, TMV; *Tobacco mosaic virus*, CaMV; *Cauliflower mosaic virus*, ToLCNDV; *Tomato leaf curl new Dehli virus*, TYMV; *Turnip yellow mosaic virus*, PPV; *Plum pox virus*, PVX; *Potato virus X*, PYV; *Potato virus Y*, WSMoV; *Watermelon silver mottle virus*, WSMV; *Wheat streak mosaic virus*, GFLV; *Grapevine fanleaf virus*, CLCuBuV; *Cotton leaf curl Borewala virus*, ToLCV; *Tomato leaf curl virus*, RBSDV; *Rice black streaked dwarf virus*, WDV; *Wheat dwarf virus*, CBSV; *Cassave brown streak virus*, UCBSV; *Uganda cassava brown streak virus*, TSWV; *Tomato spotted wilt virus*.

miR171, miR444 were specified to regulate various hormonal signaling pathways by targeting the NAC1-, ARFs-, and MADS-box respectively [114].

4. Response of plant miRNAs to bacterial infections

The involvement of plant miRNAs in defense against pathogen was primarily observed during plant-bacteria interactions. Rapid induction of miRNA393 was noticed against bacterial peptide flg22 infection in *Arabidopsis* [115,116]. The particular miRNA repress the auxin signaling by stabilizing the Aux/IAA proteins via targeting TIR1, AFB2 and AFB3 mRNAs, i.e., the F-box family genes [117]. This over-expression of miR393 reduces the growth of *Pseudomonas syringae* pv. *tomato* DC3000. Corresponding suppression of auxin signaling is also due to production of salicylic acid (SA) thus indirectly contributing to the anti-bacterial defense in plants [118,119]. Moreover, in *Arabidopsis*,

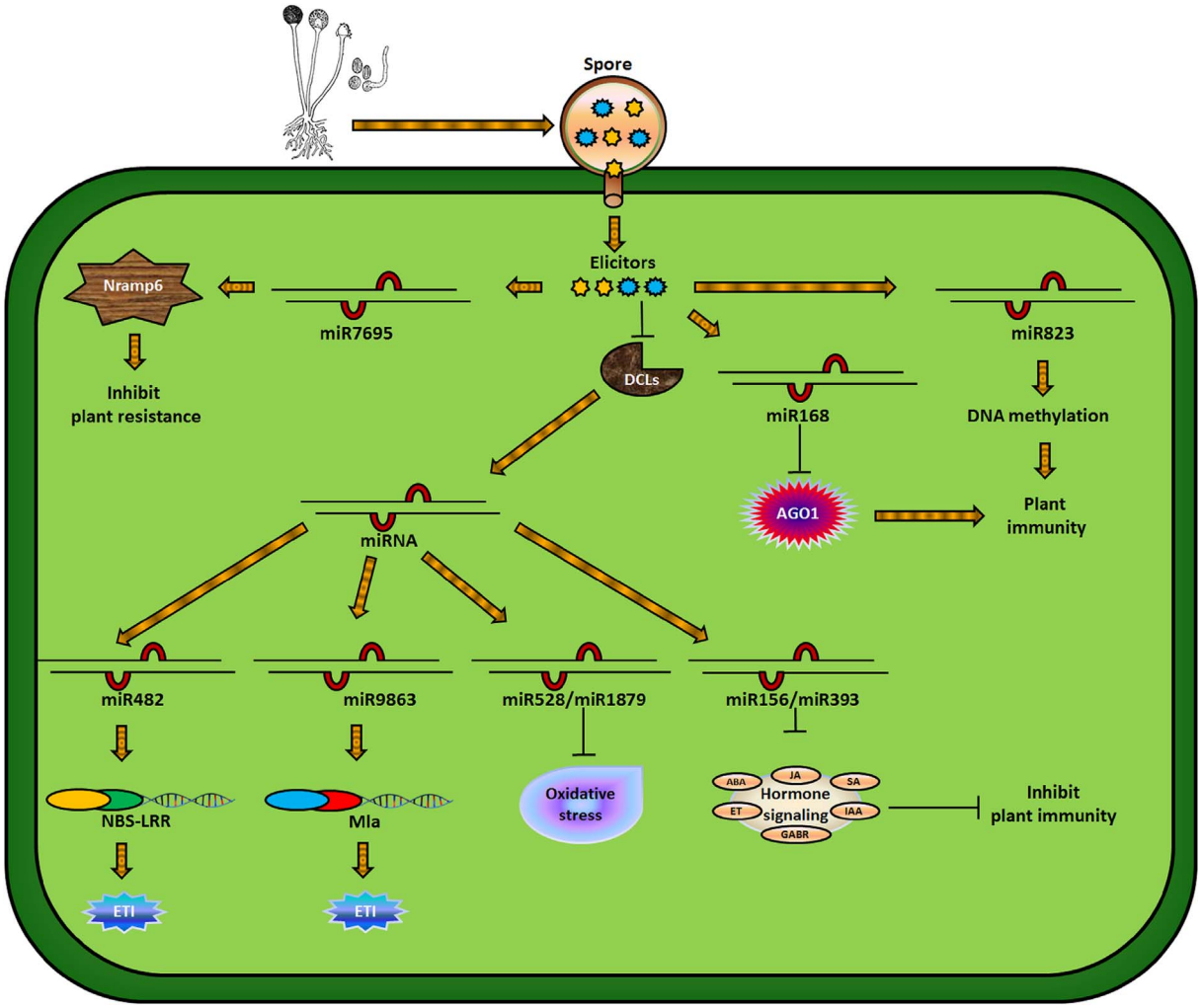

Fig. 1. Plant miRNAs regulate PTI and ETI in response to fungal infections. Fungal elicitors trigger the accumulation of different miRNAs leading towards the changes in gene expression. Higher accumulation of miR7695, miR168 and miR823 is observed during fungal infections, while miR528, miR1879, miR9863, and miR482 are down-regulated to improve plant resistance.

synergism among miR393 and SA pathway significantly contribute to enhanced tolerance against bacterial infections [120,121]. Further investigation affirmed that increased accumulation of miR393 upon bacterial infection down regulate MEMB12 (SNARE) gene encoding vacuole-localized protein involved in membrane fusion. Mutants deficient in MEMB12 presented extraordinary levels of exocytosis of the PR1 protein regulated via AGO2 [122,123]. Manipulation of host-mediated miRNAs has been observed upon the infection of various bacterial diseases (Fig. 2). Down-regulating the accumulation of pri-miR393 which is a precursor of miR393 have been documented due to the bacterial effector (AvrPtoB) [123]. This may be due to the involvement of various interfering factors during the processing of miRNA precursors. Bacterial implication regarding suppression of various RNA silencing pathways during anti-bacterial defense is the same strategy developed by viruses via utilization of several protein suppressors for interference with the silencing machinery [124,125]. Fahlgren et al. [64] reported the induction of several miRNAs during bacterial infection in *Arabidopsis* via large-scale expression profiling analysis. They found that miR160 and miR167 target the auxin-related genes, thus showing their active involvement in plant defense. They further mentioned about the down-regulation of miR162 and miR168 upon bacterial infections. These miRNAs directly target the AGO1 and DCL1 which modulate the setting up of miRNA pathways, thus insuring their activities during the bacterial defense. Interestingly, another miRNA (miR825) which is not involved in targeting any of the defense-related genes also exhibit down-regulation upon bacterial infection [126]. The activities on miR825 should be specifically targeted and researched upon as the particular miRNA may be playing any other defense-related regulatory role. Deep sequential analysis technique has helped the researcher to uncover various other miRNA families that are involved in anti-bacterial defense [127]. For example, Zhang et al. [73] described the expression of 20 diverse miRNA families upon the infection of different *Pseudomonas* strains in *Arabidopsis*. Most of these families targeted the genes directly or indirectly linked with the production and signaling pathways of various hormones such as SA, Jasmonic acid (JA) and Abscisic acid (ABA). The involvement of these hormone pathways in anti-pathogenic defense has been well documented [128–130]. For example, SA signaling pathways regulates the anti-biotrophic pathogen defense in plants while positive regulation of JA triggers and regulates the anti-necrotrophs defense [131–133]. On the other hand, ABA can have both negative and positive effects on pathogen resistance [134,135]. Thus, miRNAs facilitate the fine tuning of defense responses rather than targeting the plant immune system directly. Equivalently, massive changes in miRNA transcriptome have been observed in the *Xanthomonas axonopodis* pv. *manihotis* infected cassava plants [136,137]. Auxin response factors are the targets of mostly up-regulated miRNAs while several disease resistance genes are regulated through down-regulated miRNAs. On a similar note, callose deposition is enhanced by miR160a over-expression during defense response but miR398b and miR733 are negatively regulated during the

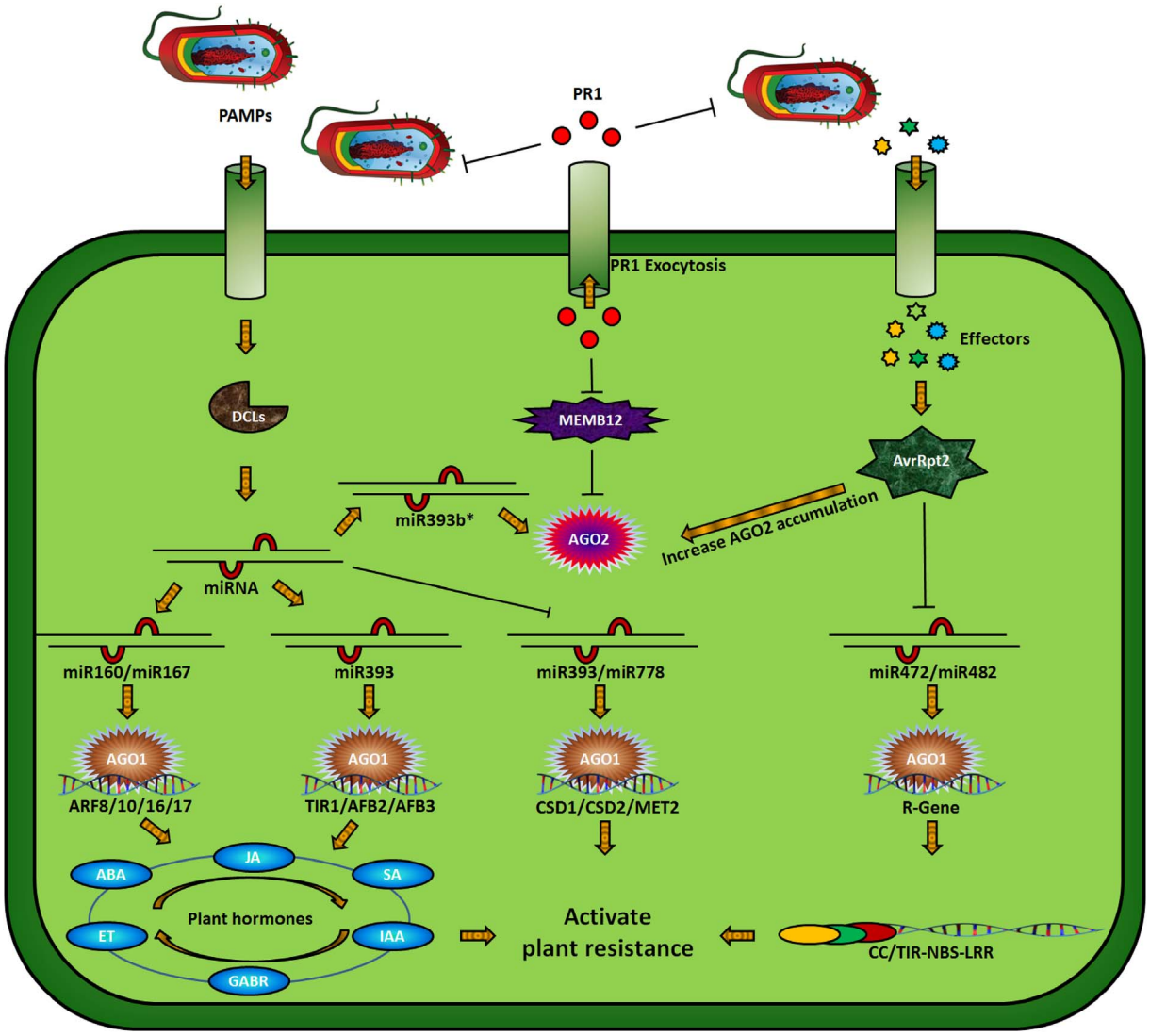

Fig. 2. Plant miRNAs actively participate in defense against bacterial attack through regulating disease resistance by fine tuning of various plant hormones. Upon the infection, plants detect PAMPs and modulate the accumulation of miRNAs. miRNAs, such as miR160, miR167 and miR393 regulate disease resistance by fine-tuning plant hormone networks, while other miRNAs (miR482/miR472) regulate the activation of R protein. miR393b* which is the pairing strand of miR393, enhances plant immunity via promoting exocytosis of antimicrobial protein.

bacterial infections [71]. Moreover, investigation of the tumors caused by the infection of *Agrobacterium tumefaciens* revealed that miR167 and miR393 were down-regulated and the mutants which were deficient in these RNA silencing specific miRNAs showed hyper-susceptibility to bacteria. Summarizing the miRNA involvement in anti-bacterial defense [138]. It has been noted that although miRNAs are one of the vital components of various defense-related pathways, yet their target specificity and direct contributions still need to be explored in most of the cases.

5. Response of plant miRNAs to virus infections

Diverse types of miRNAs are produced by various viruses which they employ for their offensive attack to generate infection of the plant cells. Oppositely, plants have discovered their defense via involving their miRNAs which occur naturally and are produced in response to any virus or viroid attack [139,140]. Initial evidence documented that *Arabidopsis* mutant *dcl1* showed the least susceptibility to RCNMV infection [141]. As DCL1 plays a preliminary role during the processing of pre-miRNAs, so the hypothetical findings support regarding the endogenous exploitation of miRNA through suppression and redirection of host gene expression. Interestingly, viral mRNA translation and RNA stability are not directly detected to be affected by miRNAs [142]. Further unveiling this phenomenon, it is assumed that miRNAs redirect viral RNAs towards replication sites. Moreover, conclusive evidences are piling up every day regarding viral gene silencing to enhance the plant immunity. Since miRNAs and siRNAs share many features in common, therefore, it is hypothesized that miRNAs may also be involved as silencing invaders. For example, miR171 directed an RNAi like process by exhibiting cleavage of mRNAs encoding scarecrow-like transcription factors in *Arabidopsis* [143]. Similarly, induction of bra-miR1885 was observed in Turnip mosaic virus (TuMV) infected Brassica [144,145]. Further analysis revealed that Toll/interleukin-1, nucleotide-binding site-leucine-rich repeat (TIR-NB-LRR) disease resistance gene was targeted by bra-miR1885 which explains about the possible origin of bra-miR1885 from inverted duplication events of TIR-NB-LRR coding genes. Correspondingly, miRNA profiling was carried out through deep sequential analysis of rice plants infected by Rice dwarf virus [RDV; double stranded (ds) RNA virus] and Rice stripe virus (RSV; RNA virus) [146,147]. Results revealed that RSV infection showed triggered miRNA accumulation along with the enhanced expression level of rice DCL and AGO genes. On the contrary, RDV

infection showed an up-regulation of OsRDR genes. However, it is still not clarified that either up-regulation of AGO, DCL or RDR genes play any role in plant defense or not. Similar studies were reported regarding the miRNA expression profiling upon the infection with the Oilseed rape mosaic tobamovirus (ORMV) in *Arabidopsis* [148]. He further documented that upon infection of the particular tobamovirus, higher accumulation of miRNAs was recorded however, no or little transcriptional changes were observed in the mRNA targets thus revealing the least involvement of mature miRNAs regarding defense against ORMV infected *Arabidopsis* plants. On a hypothesis, Chen et al. [149] conducted a deep sequential analysis of Cucumber mosaic virus (CMV) and the N5 strain of Tomato mosaic virus (ToMV) challenged tomato plants. The results were quite interesting as more than 85% miRNAs showed altered expressions but the study was not further followed to explore more about the role of these miRNAs in defense against the subjected viruses thus the exact role of these miRNAs is still elucidated. Similarly, another study focused upon the expression profiling of miRNAs in grapevine plants which were infected by Grapevine vein-clearing virus [150]. The results exhibited the down-regulation of miR169 and miR398 while up-regulation of miR168 and miR3623 upon viral infection. However, no clear evidence was recorded regarding the involvement of these miRNAs in disease resistance. Thus, more defense specified involvement of miRNAs is needed to be explored.

6. Response of plant miRNAs to nematode infections

Resistance to root-knot nematodes is mediated through expression of dsRNA in infected plants via silencing of genes involved in housekeeping or parasitism [151,152]. Sindh et al. [153] utilized the RNAi to achieve the resistance in *A. thaliana* by targeting the four parasitism-related genes of sugar beet cyst nematode (*Heterodera schachtii*). Although the complete resistance was not achieved but 23–64% reduction in number of mature nematode females in different RNAi lines was recorded. However, the *Meloidogyne incognita* induced gall formation in soybean roots was successfully reduced through suppression of various tyrosine phosphatase (TP) and mitochondrial stress-70 protein precursor (MSP) genes [154]. Moreover, disruption of post-transcriptional gene silencing (PTGS) in *Arabidopsis ago1* or *ago2* mutants subsequently minimized the infection *M. incognita* [155]. Further investigation clarified that *Arabidopsis* miR159*abc* mutant showed lower susceptibility to *M. incognita*, suggesting a role for the miR159 family in plant response to nematode infections. Several miRNAs are reportedly involved in plant-nematode interactions. For example, upon the infection of *Heterodera schachtii* in *Arabidopsis*, down-regulation of miR161, miR164, miR167a, miR172c, miR396c, miR396a,b, and miR398a was observed [156–158]. Investigation of soybean cyst nematode (SCN; *Heterodera glycines*) infected plants revealed more than 100 miRNAs of 40 diverse families for their comparative response upon the infection initiation. Further analyses presented 20 differentially expressed miRNAs between SCN resistant and susceptible soybean cultivars [159,160]. Recently, Tian et al. [161], identified 60 miRNAs belonging to 25 families which may have their active involvement in response to SCN infection. Besides, nematode-induced miRNAs likely to participate in the establishment and parasitism of feeding site respectively [157]. Over-expression of nematode-induced miRNAs and silencing of their corresponding targets, may offer significant information about plant-nematode parasitism, and grant crop plants with nematode resistance.

7. Conclusions and future prospects

Pathogens continuously threat global crop production. Recent progress in plant biology revealed significant miRNA cascades responding against pathogens. But, miRNA-mediated plant immunity is, however, incomplete and requires extensive research. In addition, investigations based on miRNA-mediated processes in plant-pathogen interactions have considerable implications in devising new strategies for disease control and ultimately improve crop productivity. miRNA can be very useful as biomarkers for disease resistance characteristics in breeding programs. miRNA-mediated gene silencing has vital significance in plant immunity. Although current understanding has already laid a foundation for developing molecular tools for crop improvements yet the molecular mechanisms of miRNA-mediated gene silencing in plants need extensive elaboration and investigation. An in-depth investigation is suggested regarding the miRNA processing procedures involving biochemical enzymes and miRNA recruiting machinery. Additionally, explanation of the molecular mechanisms of interactions between plants and pathogens with particular reference to miRNAs will facilitate us to get more benefits derived from the miRNA-mediated mechanism.

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