Biologia (2018) 73:285–294
https://doi.org/10.2478/s11756-018-0034-5

REVIEW

Plant small RNAs: definition, classification and response against stresses

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Received: 20 December 2017 / Accepted: 22 February 2018 / Published online: 7 March 2018

Abstract

Gene knockdown and gene-silencing pathways in eukaryotic organisms are associated with small RNAs 20 to 25 nucleotides in length, which include microRNAs (miRNAs) and small interfering RNAs (siRNAs). These small RNAs are recruited to repress gene expression upstream or downstream of the transcription pathway. RNA interference (RNAi) is a biological inhibitor of gene expression that results in the destruction of messenger RNAs (mRNAs), leading to the inhibition of protein production. Indeed, RNA silencing plays a key role in plant development in terms of the plant's response to both biotic and abiotic stresses. Conversely, Viral Suppressors of RNA silencing (VSRs) are proteins that hamper antiviral RNAi activation in plants, lead to suppress plant RNA-silencing. These VSR proteins prevent the induction of the plant antiviral RNAi immune response. This review focuses on small RNAs in plants and their roles in the responses of plants to biotic and abiotic stresses.

Keywords RNA silencing · RNAi · miRNA · siRNA · Dicer · RISC · VSR

Abbreviations

RNA	ribonucleic acid
mRNA	messenger RNA
RNAi	RNA interference
miRNA	microRNA
RSS	RNA silencing suppressor
dsRNA	double-stranded RNA
Pol II	RNA polymerase II
Pol III	RNA polymerase III
RNase III	ribonuclease III
RISC-miRNA	RImR
tRNA	transfer RNA
RdRp	RNA-dependent RNA polymerase

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Electronic supplementary material The online version of this article (https://doi.org/10.2478/s11756-018-0034-5) contains supplementary material, which is available to authorized users.

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Introduction

Small non-coding RNAs (sncRNAs), which are 20–25 nucleotides, are vital regulators of gene expression. In plants, gene regulation through sncRNAs is involved in the plant's response and adaptation to abnormal conditions through either transcriptional gene silencing (TGS) or post-transcriptional gene silencing (PTGS) (Covarrubias and Reyes 2010). These sncRNAs interfere with messenger RNA (mRNA) translation, leading to the regulation of various biological processes (Axtell and Bowman 2008). In eukaryotes, sncRNAs are divided into two important groups, according to their biogenesis and functions: microRNAs (miRNAs) and small interfering RNAs (siRNAs). These sncRNAs are highly conserved regulators of gene expression in both plants and animals (Liu and Paroo 2010). In plants, RNA silencing plays crucial roles not only at the endogenous level (such as repetitive genomic sequences and transposons), but also at the exogenous level (Carthew and Sontheimer 2009; Martinez de Alba et al. 2013). "RNA silencing" was subsequently used as a term for specific inhibition pathways mediated by small RNAs. This mechanism was mediated at the TGS level, either through DNA methylation and chromatin modification, or at the PTGS level through RNA cleavage and repression (Martinez de Alba et al. 2013; Movahedi et al. 2015a). In oppose of sncRNAs, long non-coding RNAs (lncRNAs) are polyadenylated and capped RNAs with more than 200 nucleotides (Yang et al. 2015). Furthermore, lncRNAs involved in

PTGS or TGS enable to combine with siRNAs, TFs (Transcription factors) and DNA leading to remodel chromatin, histone modification and direct de novo DNA methylation in response to biotic or abiotic stresses (Wang et al. 2017).

MicroRNAs

Firstly, the downregulation of miRNAs was discovered in nematode worm *Caenorhabditis elegans* (Lee et al. 1993). This function was first described in plants (Arabidopsis) when it was improved that JAW miRNA is involved in the regulation of shape of leaves (Palatnik et al. 2003). MicroRNAs are major regulatory molecules that share several properties with siRNAs (Xie et al. 2015). In eukaryotic organisms, microRNAs, which are noncoding and single-stranded RNAs, target mRNAs to play important roles in response to various stresses and plant development based on morphological and physiological processes (Jian et al. 2017; Stepien et al. 2017). In addition, recent reports have showed that complex miRNAs are involved in salt and drought stresses based on hormone regulation during seed germination (Ruiz-Ferrer and Voinnet 2009; Jian et al. 2016). RNA polymerase II (Pol II) transcribes nuclear- encoded *MIR* genes resulting in forming hairpin primary miRNAs (pri-miRNAs) (Khraiwesh et al. 2012). In plants, Pri-miRNAs include a lower stem around 15 nucleotides under duplex miRNA area, followed by an internal loop (Fig. 1, miRNA) (Werner et al. 2010). Studies also revealed that the lower stem is an appropriate position for binding the Dicer-like protein 1 (DCL1) cleavage enzyme (Fig. 1, miRNA) (Werner et al. 2010).

The DAWDLE, a DCL1-interacting protein, interacts with primary miRNAs (pri-miRNAs) to form a stable molecule, followed by linking of Cap-binding protein (CBP20/80) at the 5′ cap section (Nicolas et al. 2012). The complex of DCL1, zinc finger protein serrate (SE), HYL1, and CBP20/80 proteins bends pri-mRNA at the 5′-end to form a d-body structure (Fig. 1) (Nicolas et al. 2012). In the first cleavage, DCL1 dices pri-miRNA to separate lower stem to form precursor miRNA (pre-miRNA) (Fig. 1, miRNA). DCL1 then catalyzes the second cleavage to separate the terminal loop and upper stem from pri-miRNA to generate duplex pre-miRNA, a substrate for Hua Enhancer 1 (HEN1) (Fig. 1, miRNA). HEN1, a nuclear methyltransferase, prevents duplex pre-miRNA by methylating the 3′ end from each strand with a 2’-O-methyl group of the degradation (Nicolas et al. 2012), leading to produce miRNA/miRNA duplexes. Then, the exportin-5 homologue HASTY translocates methylated miRNA/miRNA duplexes from the nucleus into the cytoplasm to bind the appropriated mRNA (Fig. 1).

The function of miRNAs frequently occur through binding to the 3’-UTR region of mRNA to suppress translation or in the coding region to prevent the function of RNA polymerase (Fig. 2) (Cuperus et al. 2011; Nicolas et al. 2012).

In the cytoplasm, RNA-induced silencing complex (RISC), which contains Argonaute 1 (AGO1) as the RNA slicer, loads miRNA onto target mRNA by forming an RISC-miRNA (RImR) complex. As shown in Fig. 2, the RImR enable to disrupt protein translation at coding and non-coding (3’-UTR) regions of mRNA. Through non-coding region, RImR inhibits of initiating binding protein complex involved in translation. Binding protein complex, poly-A binding protein (PABPC1), m7G-cap binding protein (eIF4E), and translating factor (eIF4F), forms an mRNA loop that leads to protein translation in the absence of miRNA. Furthermore, RImR inhibits of either initiation subunits of ribosome (60s and 40s) on mRNA or translating protein by connected ribosome. On the other hand and through coding region, RImR recruits the SQN and HSP90 proteins to splice mRNA by AGO1 directly, and leading to RNAi.

Responsive miRNAs against stresses

Regulatory miRNAs respond to biotic and abiotic environmental stresses, including salinity, drought, cold, and fungal and bacterial infections (Zhou et al. 2008, 2010; Ram and Sharma 2013; Sun et al. 2015). Micro RNAs often control hormone signaling in plants to make a resistance against salt stress. For instance, salt stress stimulates *miR393* that is enable to knockdown the expression of *AFB2* and *TIR* genes, which are responsible for increasing tolerance against salinity (Supplementary 1) (Navarro et al. 2006). Iglesias et al. (2014) have reported that *miR395* targets the genes that encode superoxide dismutase, laccase, and ATP sulfurylases (APS1/2/3/4). These researchers have stated that various environmental factors lead to the induction of miRNAs. Other miRNAs such as *miR393*, *miR397b* and *miR401* regulate the plant response to drought, abscisic acid (ABA), cold, and salt stresses (Fileccia et al. 2017). In addition, *miR319c* is induced only by cold, while *miR389a* is downregulated by all stresses (Fileccia et al. 2017). Recently, 48 miRNAs were detected in *Populus trichocarpa* that regulate the genes, which are dependent on developmental processes and stress responses (Kitazumi et al. 2015).

Achard et al. (2004) reported that both gibberellic acid (GA) and ABA regulate the expression of *miR159* (Supplementary 1). In addition, ABA regulates the expression of *miR160, miR169 and miR398* (Supplementary 1) (Jung and Kang 2007; Liu et al. 2007; Li et al. 2008; Jia et al. 2009).

(Liu et al. 2008) reported that *miR167*, *miR393*, and *miR171* are involved in responses to abiotic stresses such as salinity and H_2O_2 (Fig. 3). Liu et al. (2008) also reported that in *Arabidopsis thaliana,* 35 miRNAs are upregulated by salt stress (Fig. 3). Baek et al. (2016) reported that in *Arabidopsis thaliana*, the regulator *miR399f* is involved in salt, drought, and ABA signaling (Fig. 3, supplementary 1).

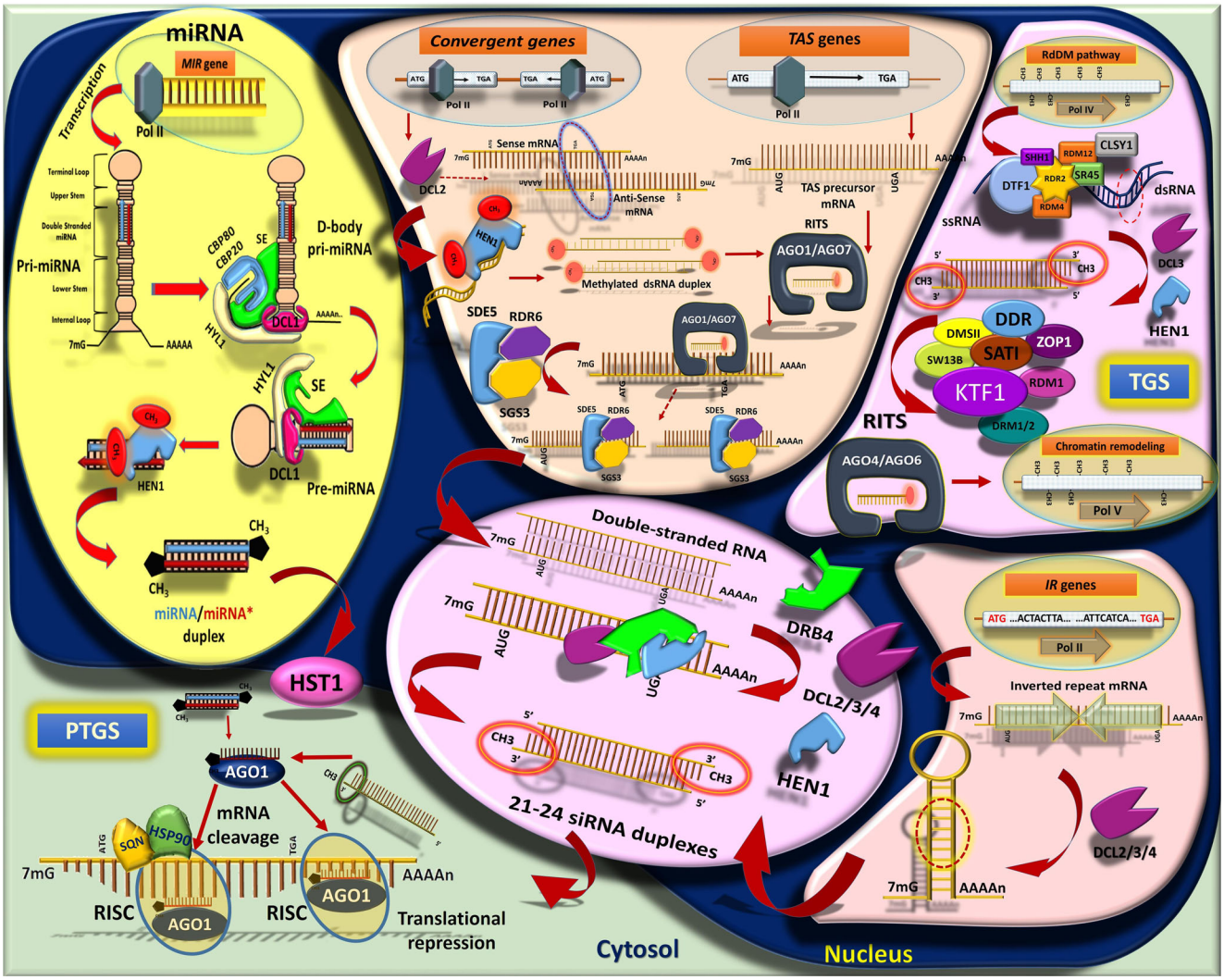

Fig. 1 Small RNA pathways in plants: 1) RNA PolII transcribes non-coding *MIR* genes to form hairpin primary miRNAs. The complex of DCL1, HYL1, SE, and CBP20 or CBP80 (DHSC) proteins binds to pri-miRNAs to form a D-body structure. DCL1 dices pri-miRNAs to form precursor miRNAs (pre-miRNA). HEN1 methylates miRNA/miRNA* duplex to prevent their degradation. Hasty proteins transfer the duplex from the nucleoplasm to the cytoplasm. RISC guides miRNA/miRNA* duplex to the target mRNA. 2) Convergent genes: Pol II forms dsRNA. DCL2 processes dsRNA into nat-siRNAs. 3) *Trans-acting* siRNAs: First, PolII transcribes non-coding *TAS* genes. TAS precursor mRNA generates an appropriate substrate for recruiting RDR6, SGS3, and SDE5. This results in the generation of dsRNAs. In the nucleus, DCL4 and DRB4 cooperate to dice dsRNA, leading to generate secondary 21-nucleotide ta-siRNAs. The HEN1 protein prevents ta-siRNA duplexes by methylating. AGO1 proteins are loaded onto ta-siRNA duplexes, which are transferred into the cytoplasm, leading to the suppression of the target mRNA. 3) RdDM pathway: PolIV transcribes particular regions of the genome, such as methylated DNA, repetitive sequences, and transposons, to form ssRNA. DTF1 recruits RDR2, RDM4, SR45, SHH1, and CLSY1 proteins to convert ssRNA to dsRNA. DCL3 processes dsRNA to 24-nucleotide-long siRNAs. AGO4/6/9 associates with siRNAs to form RITS complex. PolV transcribes scaffold RNA to recruit RITS, RDM1, KTF1, DDR, ZOP1, DMSII, SW13B, and DRM1/2 for transfering methyl groups to remodel chromatin, leading to gene silencing. 4) endoIR-siRNA: Pol II transcribes genes that contain long inverted repeat sequences to form hairpin dsRNAs. DCL2, 3, and 4 dice this hairpin in the sense-antisense region to form endoIR-siRNAs. HEN1 then methylates endoIR-siRNA duplexes to prevent their degradation. Finally, the RISC complex containing AGO1 loads onto endoIR-siRNA, leading to the suppression of the target mRNA

Recent researches have been reported that in plants, abiotic stresses show different regulations on miRNAs (Song et al. 2013; Fang et al. 2014; Chen et al. 2015; Hajyzadeh et al. 2015). When the *miR156, miR159, miR164, miR168*, *miR170* are downregulated by abiotic stresses resulting in decreasing of tolerance of plants against environmental stresses, the *miR169, miR171, miR319, miR395, miR408* are upregulated by abiotic stresses resulting in increasing of tolerance of plant against environmental stresses (Song et al. 2013; Fang et al. 2014; Chen et al. 2015; Hajyzadeh et al. 2015). Liu et al. (2008) reported that the functions of some miRNAs differ among plant species. For example, in Arabidopsis, the *miR156, miR159* and *miR168* are upregulated in response to salt stress (Fig. 3). Furthermore, in *Oryza sativa*, the *miR169* and *miR397* are upregulated in

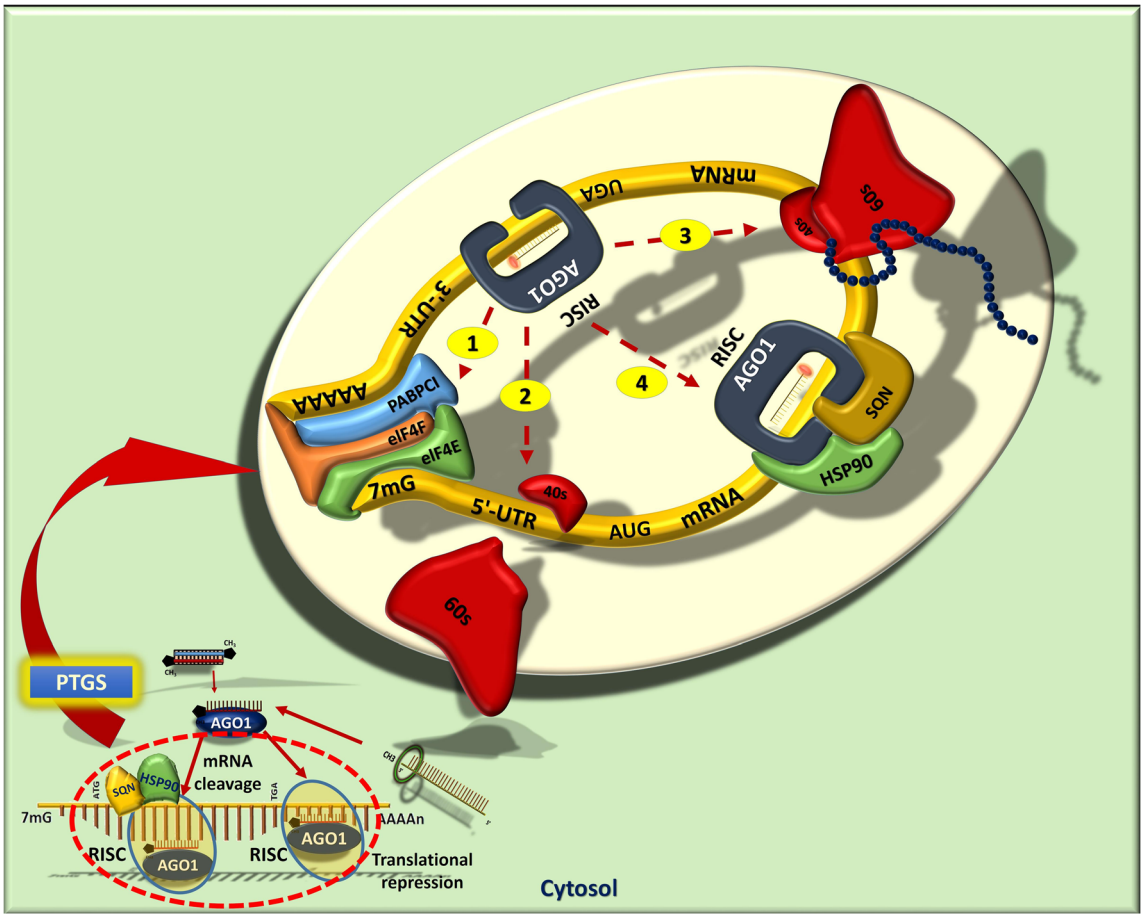

Fig. 2 Post transcriptional gene silencing (PTGS): 1) RImR inhibits of initiating binding protein complex involved in translation. 2) RImR inhibits of initiation subunits 60s and 40s of ribosome. 3) RImR inhibits protein translation. 4) RImR at the coding region recruits the SQN and HSP90 proteins to splice mRNA by AGO1, leading to RNAi

response to cold stress (Zhou et al. 2008) (Supplementary 1). Studies on poplar indicated that the *miR168a*, *b*, and *miR477a, b* are upregulated, whereas *miR475a, b, miR476a, and miR156g-j* are downregulated in response to cold stress (Rossi et al. 2015). In addition, in Arabidopsis the *miR165, miR166, miR396, miR393*, and *miR408* are downregulated in response to cold stress (Liu et al. 2008) (Fig. 3). Biotic and abiotic stresses lead to the accumulation of reactive oxygen species (ROS) such as superoxide dismutase (SOD), guaiacol peroxidase (POD), and catalase (CAT) resulting in increasing levels of H_2O_2, $\bar{O}_2$, and hydroxyl radicals (Liu et al. 2009; Li et al. 2011; Movahedi et al. 2015b, c; Rossi et al. 2015). Plants respond to biotic and abiotic stresses by producing enzymatic and non-enzymatic antioxidant molecules that scavenge ROS (Movahedi et al. 2015b). In Arabidopsis, *miR398* targets CSD1/2/3 genes to regulate the expression of Cu-Zn SODs (Iglesias et al. 2014) (Supplementary 1). Kitazumi et al. (2015) reported that the accumulation of Cu-Zn SOD results in downregulation of transcription of CSD1/2/3 proteins due to expression of miR398. Yamasaki et al. (2007) explained that to synthesize the required proteins, Cu^2+ stimulates the expression of *miR398* to remove Cu^2+ from Cu-Zn SODs. In rice, H_2O_2 accumulation leads to upregulation of *miR169*, *miR397, miR827*, and *miR1425*, and downregulation of *miR528*, which directs the cell to increase its ROS-scavenging activity (Li et al. 2011).

Small interfering RNAs

In plants, 70–80-nucleotide-long transcript mRNAs generate stem-loop structures as a substrate for DCL proteins to cut the stems of dsRNA for the production of siRNAs (Bartel 2009; Voinnet 2009; Cuperus et al. 2011; Nicolas et al. 2012). Then, nuclear HEN1 methylates siRNAs to prevent their degradation. In addition, the RISC complex binds to and unwinds double-stranded siRNAs through its helicase activity (Guleria et al. 2011). Finally, the PAZ domain, which comprises a complex of Ago, a P-element induced wimpy testis (PIWI), and Zwille, associates with siRNAs to direct them toward mRNA molecules with endonuclease activity (Arribas-Hernandez et al. 2016). Double-stranded RNAs, necessary for production of siRNAs, are generated from a variety of sources. These include natural cis-antisense transcripts, trans-acting siRNAs, endogenous inverted repeated DNA,

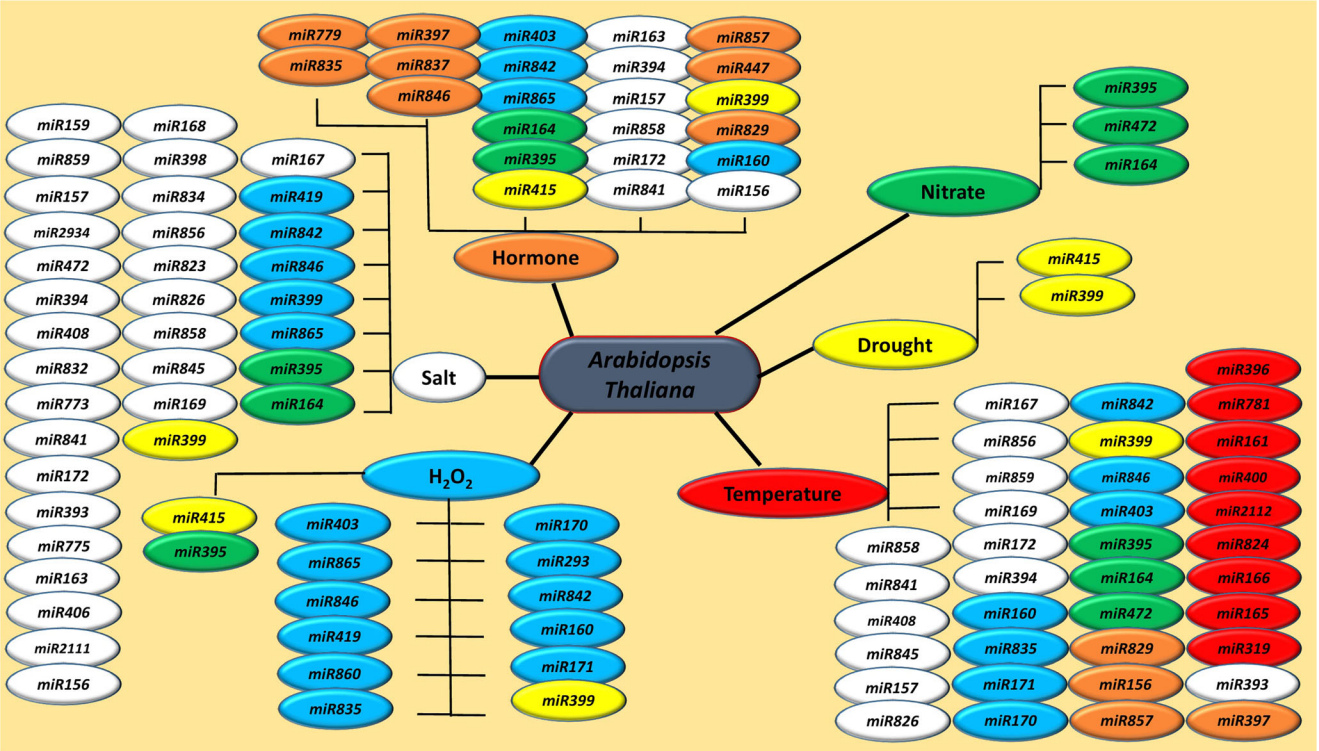

Fig. 3 Schematic of miRNAs included in abiotic stresses in *Arabidopsis thaliana*. Shared colors represent the same miRNAs in different stresses

the RdDM pathway, and viral RNAs. SiRNAs move cell to cell throughout whole the plant to facilitate systemic RNA silencing (Serra-Soriano et al. 2017). Small interfering RNAs are divided into trans-acting small interfering RNAs (tasiRNAs), secondary transitive siRNAs, long small interfering RNAs (lsiRNAs), heterochromatic small interfering RNAs (hcsiRNAs), primary siRNAs, natural antisense transcript-derived small interfering RNAs (nat-siRNAs), and repeat associated small interfering RNAs (ra-siRNAs) (Ramachandran and Chen 2008; Ghildiyal and Zamore 2009; Contreras-Cubas et al. 2012; Wei et al. 2012; Bulgakov and Avramenko 2015; Conti et al. 2017; Tsuzuki and Watanabe 2017).

Classification of siRNAs

Cis-natural antisense siRNAs

Convergent genes are complementary strands of DNA at the same locus that transcribe cis-natural antisense transcripts (cis-NATs) (Martinez de Alba et al. 2013). Cis-NATs generate dsRNA precursors, which activate DCL2, leading to form nat-siRNAs. The complementary sense and antisense sequences from Cis-NATs genes transcribe to mRNAs, leading to overlap close to the stop codon and form a dsRNA at the 3′-end area (Bouchard et al. 2015). Katiyar-Agarwal et al. (2006) reported that in the first step AGO proteins load on the primary nat-siRNAs to cleave the expressed complementary transcript, resulting in the formation of nat-ssRNAs. Katiyar-Agarwal et al. (2006) also reported that in the second step PolIV, RNA-dependent RNA polymerase 6 (RDR6), and the RNA binding suppressor of gene silencing 3 protein (SGS3), which protects fragments against degradation, are recruited to convert ssRNA to dsRNA, resulting in the generation of 21-nucleotide nat-siRNAs. Finally, exportin-5 homologue HASTY, transfers the nat-siRNAs from the nucleus to the cytoplasm, thereby suppressing the expression of the target mRNA by PTGS (Fig. 1).

Trans-acting siRNAs

Plants possess long, non-coding transcripts drive the production of *trans-acting* siRNAs (ta-siRNA) encoded by *trans-acting* siRNA (TAS) genes (Wu 2013). Jauvion et al. (2010) reported that in plants there exist four types of *TAS* loci and three important miRNAs involved in the ta-siRNA pathway. Jauvion et al. (2010) also stated that THO/TREX complexes transfer long non-coding RNAs to the AGO/miRNA complex, leading to loading of AGO1 on two miRNAs (*miR173* and *miR823*) and AGO7 on *miR390*, resulting in cleavage of their RNA target at the *TAS* locus. In the ta-siRNA pathway, SGS3 recruits RDR6 and the putative RNA export factor SDE5 to convert the RNA precursor to dsRNA (Elmayan et al. 2009). Then, the DCL4 protein recruits the DRB4 protein to dice dsRNA, resulting in generating 21-nucleotide ta-siRNAs (Elmayan et al. 2009). The HEN1 protein methylate

siRNA duplexes to prevent of degradation and transfer them to the cytoplasm (Fig. 1). Wu (2013) reported that AGO1 is loaded onto ta-siRNA to guide cleavage of the target mRNA in PTGS.

SiRNAs dependent on RdDM

Repetitive sequences and transposons are two important triggers of the RdDM pathway, which is dependent on DNA-directed RNA polymerase IV (PolIV) and DNA-directed RNA polymerase V (PolV), together with 20–24-nucleotide siRNAs (Movahedi et al. 2015a). Recent studies have shown that AGO4/6/9 is loaded onto methylated, single-stranded siRNA to trigger de novo methylation and transcriptional silencing of transposons and repetitive sequences (Martinez de Alba et al. 2013; Zhu et al. 2013). It has been shown that the functions of AGO proteins are on the basis of their expression and target (Havecker et al. 2010). For instance, AGO4 expresses in buds and roots whereas AGO6 expresses in shoots and roots, particularly the apical meristem (Havecker et al. 2010). PolIV recruits CLSY1, SAWADEE HOMEODOMAIN HOMOLOG 1 (SHH1), and DNA Transcription Factor 1 (DTF1), which are encoded by the plant-specific gene DTF1 to detect histone H3K9me2 (Law et al. 2013) (Fig. 1).

In addition, RNA-dependent RNA polymerase 2 (RDR2) associates with RNA-directed DNA methylation 4/12 (RDM4/12) and SR45, which is an enhancer enzyme, to convert ssRNAs to dsRNAs (Zhu et al. 2013; Movahedi et al. 2015a). Then, DCL3 dices dsRNAs to form 24-nucleotide siRNA duplexes, which recruit HEN1, resulting in the generation of methylated 3′ overhang siRNA duplexes (Law et al. 2013; Movahedi et al. 2015a). RNA-induced transcriptional silencing (RITS), which involves AGO4/6/9, then guides methylated siRNAs onto RNA scaffolds directed by PolV (Law et al. 2013). The DDR complex, including RNA-directed DNA methylation 1 (DRD1), Defective Meristem Silencing 3/11 (DMS3/11), and RDM1, associates with RITS and PolV and mediates the recruitment of SW13B protein to the scaffold RNA, which facilitates regulation of the interactions between siRNAs and scaffold RNA and stabilizes the nucleosome position (Law et al. 2011). Finally, the RITS interacts with Kow-domain-containing transcription factor 1 (KTF1) and associates with RDM16 and the splicing factors STA1 and POZ1 to recruit domain rearranged methyltransferase 2 (DRM2), leading to DNA methylation at the target loci and chromatin remodeling (Movahedi et al. 2015a) (Fig. 1).

SiRNAs dependent on endogenous genes

Some endogenous genes, including inverted-repeated sequences, at various loci are transcribed to form single-stranded hairpin precursor RNAs and drive the production of endoIR-siRNAs (Martinez de Alba et al. 2013). According to the Dunoyer et al. (2010), two inverted-repeat sequence genes (IR71 and IR2039) encode hairpin mRNAs, resulting in the generation of 21–24-nucleotide siRNAs following the recruitment of DCL2/3/4 (Fig. 1). According to the Dunoyer et al. (2010) endoIR-siRNAs are enable to trigger RNA silencing.

Responsive siRNAs against stresses

Abiotic stress

Borsani et al. (2005), while working on nat-siRNAs in Arabidopsis, discovered that SR05 and P5CDH proteins play a key role in protection against oxidative and osmotic stresses under high-salt conditions. Borsani et al. (2005) also reported that while *SR05* gene is only induced by salt stress, *P5CDH* gene is fundamentally expressed. In addition, high salt stress causes to produce 24-nt nat-siRNAs corresponding to the transcribed mRNA of *SR05* gene, leading to target the transcribed mRNA of *P5CDH* gene to degrade for producing 21-nt nat-siRNAs.

Borsani et al. (2005) demonstrated that 21-nt nat-siRNAs corresponding to *P5CDH* gene downregulate accumulation of proline, leading to promote tolerance against salt stress. Conversely and in the absence of P5CDH activity, PC5 (a toxic metabolite) and ROS accumulate and damage plant cells. In contrast, increased levels of PC5 and ROS upregulate the production of the detoxifying protein SR05, resulting in resistance to salt stress. Borsani et al. (2005) indicated that nat-siRNAs, which are derived by *SR05* and *P5CDH* genes, regulate ROS production under abiotic stresses. Furthermore, in wheat seedlings, siRNA007927_0100_2975.1 is downregulated by abiotic stresses such as cold, drought, and salt. In contrast, Yao et al. (2010) exhibited that heat downregulated siRNA080621_1340_0098.1 and cold upregulated it. In addition, in wheat seedlings, siRNA005047_0654_1904.1 is downregulated by drought, heat, and salt stresses and upregulated by cold, while Yao et al. (2010) presented that drought, heat, and salt stresses downregulate siRNA002061_0636_3054.1. Ben Amor et al. (2009) reported that some long non-protein-coding RNAs (npcRNA) are involved in the responses to biotic and abiotic stresses. Moreover, salt stress increases the accumulation of npcRNA536 and npcRNA60, but decreases the npcRNA82 and npcRNA72. Furini et al. (1997) identified that in *Craterostigma plantagineum*, the endoIR-siRNAs dependent on constitutively desiccation tolerant-1 (CDT-1) are involved in ABA dehydration stress and enhance plant tolerance to desiccation.

Biotic stress

Nat-siRNAATGB2 is an endogenous siRNA involved in the responses of plants to biotic stresses (Katiyar-Agarwal et al. 2006). *Nat-siRNAATGB2* regulates the effector-triggered

immunity (ETI) protein, which is encoded by the *R* gene, and represses the expression of the antisense of pentatricopeptide repeats protein like gene (PPRL, At4g35850) mRNA, a negative regulator of RPS2 against *Ps pathovar tomato* (*Pst*) (strain DC3000) (Katiyar-Agarwal et al. 2006). Katiyar-Agarwal et al. (2006) identified a plant endogenous long siRNA (lsiRNA) comprising 30–40 nucleotides. These lsiRNAs were induced by bacterial infection. These authors also classified AtlsiRNAs according to the infections of *Pst* and plant false growth conditions (conditions that direct plants to damage, such as environmental stresses). In this classification, *Pst* infections strongly induce AtlsiRNA1, but moderately induce AtlsiRNA2/3/4. Plant false growth conditions also induce AtlsiRNA2/3/4. Hewezi et al. (2008) demonstrated that infection by the *Heterodera schachtii* upregulated the siRNA41, siRNA46, and siRNA9, but downregulated siRNA32.

Viral suppressors of RNAi

Definition and mechanism

An important RNAi pathway is dedicated to the control of exogenous nucleic acids, which originate mostly from plant viruses. Viral suppressors of RNA silencing (VSRs) are proteins that hamper antiviral RNAi activation in plants, and so contribute to the subversion of plant immunity (Murray et al. 2013). Indeed, VSRs inhibit RNA silencing (Shen et al. 2015). Many viruses express VSRs or RNA silencing suppressor (RSS) molecules to block the antiviral RNAi pathway (Calil and Fontes 2017). Baulcombe (2015) reported that the core of the RNAi mechanism includes the conversion of viral dsRNAs to siRNAs, catalyzed by DCL proteins. These siRNAs direct AGO to inhibit RNA translation or RNA replication. Martinez de Alba et al. (2013) also reported that RNA polymerase II binds to the promoter of the viral DNA to generate mRNA from the integrated transgene. Then, RDR protein generates dsRNA, leading to the formation of 21–22-nucleotide-long siRNA duplexes, which are diced by DCL2/4 and methylated by HEN1 to initiate PTGS. According to the Martinez de Alba et al. (2013), in plants, viral replication drives PTGS. Most of these proteins bind to dsRNAs and siRNA duplexes to suppress the antiviral RNAi pathway (Merai et al. 2006; Murray et al. 2013). Example VSRs include NSs of tosposviruses (Bucher et al. 2003), the NS3 of tenuiviruses (Xiong et al. 2009), the P24 of vitiviruses (Li et al. 2018), and the joint function of HcPro and P1 from potyviruses (Lakatos et al. 2006; Valli et al. 2007). In the functional step, the 2b protein of cucumoviruses binds to AGO to prevent cleavage of target mRNA by RISC (Zhang et al. 2006; Cenik and Zamore 2011) and the P0 of poleroviruses degrades AGO (Baumberger et al. 2007). The 16 k protein of tobraviruses (Martin-Hernandez and Baulcombe 2008; Bruckner et al. 2017), and P30 of tobamoviruses (Ding and Voinnet 2007) inhibit signaling among cells of the immune system. More than 40 types of VSR are recognized (Murray et al. 2013). Potyviruses have specific VSRs, including HcPro protein, which produce proteolytic polyproteins to suppress plant RNAi (Rajamäki et al. 2004). The VSRs P19 and 2b are present in tomato bushy stunt and cucumber mosaic viruses, respectively (Ding and Voinnet 2007). For example, the 2b protein binds to a 25-nucleotide dsRNA in cucumber mosaic viruses to inhibit general RNA silencing. In addition, this VSR prevents duplex siRNAs from binding to RISC, thus leading to an increased concentration of viruses (Ding and Voinnet 2007).

The HcPro protein is a VSR that inhibits the functions of 21-nucleotide siRNAs (Merai et al. 2006; Murray et al. 2013). HcPro possibly methylates the 3′ end of 21–22-nucleotide siRNAs, which decreases their stability and leads to their degradation (Ebhardt et al. 2005). Furthermore, the P0 protein is a VSR that harbors an F-box motif, which is a target for ubiquitin ligase SCF E3, interacts with orthologous SKP1, ubiquitin-involved ligase E3, and inhibits plant RNA silencing (Mangwende et al. 2009). The P19 protein, a tomato bushy stunt VSR, binds tightly to 20- or 22-nucleotide siRNA duplexes, inhibiting their binding to RISC (Ding and Voinnet 2007).

Conclusions

Complete identification of target genes enhances our understanding of the activities of small RNAs in plants. Small RNAs are critical factors in regulatory of genome. Most small RNAs, which are involved in RNAi pathways, were identified during genetic diversity and TGS or PTGS studies. An important remained question is why some small RNAs can be transported from their cell of origin, but others cannot? The answer to this question will facilitate control of RNAi, miRNA, and siRNA networks.

Acknowledgments This work was supported by the National Key Program on Transgenic Research (2018ZX08021001), the National Science Foundation of China (No. 31570650), and the Priority Academic Program Development of Jiangsu Higher Education Institutions.

Author contributions In this review, A.M. directed all the authors. In addition, J.Z. and W.S. contributed equally as the first author. The other authors attempted to read papers and gather information for this manuscript. All authors drafted and approved the manuscript.

Compliance with ethical standards

Conflicts of interest The authors declare no conflict of interest.

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