



REVIEW

# Implications of small RNAs in plant development, abiotic stress response and crop improvement in changing climate

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Received: 12 July 2023 / Accepted: 10 October 2023 / Published online: 15 November 2023  
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## Abstract

RNA sequencing technology has revealed a vast number of small RNAs (sRNAs) involved in plant development, stress management, and crop improvement. With improvements in molecular biology techniques and bioinformatic tools, sRNAs and their regulations have taken a mainstream position in various research fields, including plant science. Moreover, recent findings emphasize the significance of ncRNAs and sRNAs in spliceosome machinery. Non-coding RNAs in plants consist of ribosomal RNAs (rRNAs), transfer RNAs (tRNAs), small nucleolar RNAs (snoRNAs), small nuclear RNAs (snRNAs), microRNAs (miRNAs) (19–25 nt), short interfering RNAs (21–23 nt), and long non-coding RNAs (lncRNAs) (over 200 nt). The miRNAs and siRNAs have similar sizes but originate from structurally different RNA molecules and follow distinct biogenesis pathways with different modes of action. Uncovering their impact on plant developmental patterns and stress regulatory mechanisms assumed paramount importance in plant stress biology, specifically projects focused on crop improvement. Plants constantly face and adapt to environmental stresses that hinder their growth and development. Adverse effects of abiotic stresses, such as drought, heat, cold, and salinity, on plant productivity are well documented. With the onset of environmental stresses, certain sRNAs and ncRNAs take up prominent roles in cellular homeostasis and coordinate the stress responses. This review explores the functions of sRNAs and their interactions during plant development and stress regulation. The theme of this paper becomes pertinent given the challenge of developing crops for future environments.

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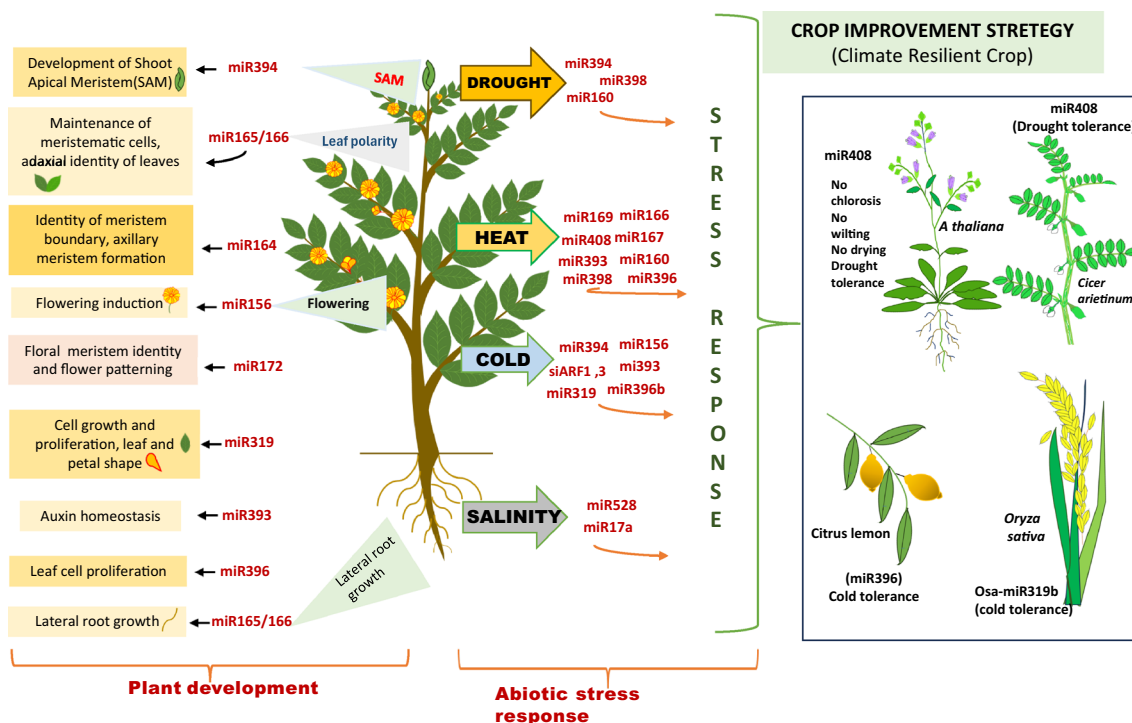
Corresponding Editor: Sachin Rustagi; Reviewers: Anjana Rustagi, Neeraj Kumar Vasistha.

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## Graphical abstract



**Keywords** RNA sequencing · Small RNA · Non-coding RNA · Micro RNA · Small interfering RNA · Abiotic stress · Crop improvement

## Introduction

Spectacular developments in the RNA world in the past few decades have contributed significantly to a better understanding of genomics and transcriptomics. Among them, the implications of non-coding and small RNAs assumed great importance in plant development, specifically tissue patterning, stress regulatory mechanism, and crop improvement, under rapidly changing climatic conditions [17, 92]. The non-coding RNAs (ncRNAs) include ribosomal RNA (rRNA), transfer RNA (tRNA), small nuclear RNA (snRNA) in spliceosome machinery, and regulatory non-coding RNAs. Where regulatory non-coding RNAs are categorized into micro RNAs (miRNAs, 19–25nt), small interfering RNAs (siRNAs, 21–23nt), and long non-coding RNA (lncRNAs, > 200 nt) in plants [7, 20, 66, 74]. Although miRNA and siRNA have somewhat similar sizes, they originate from two different precursor structures and follow different biogenesis pathways with varied modes of action [8, 99]. Long non-coding RNAs act as a source of miRNAs and also function as regulatory factors, whereas Phased small interfering RNAs (phasiRNAs) are produced from lncRNAs under the regulation of miRNA [10]. In the recent past, the

study of small RNAs, especially their primary regulations, gained popularity due to their varied roles reported from diverse research fields.

In 1998, Fire et al. reported a breakthrough process of sequence-specific endogenous gene silencing from *Caenorhabditis elegans* under the act of long double-stranded RNAs (dsRNAs), subsequently popularized as RNA interference (RNAi) or RNA silencing [26, 39]. The process of RNAi involves siRNAs and miRNAs, which is an outcome of double-strand RNA cleavage effected by DICER (ribonuclease) or a Dicer-like protein (DCL) [62]. Later, such miRNAs were also found and reported from *Arabidopsis* [62, 88, 111]. Till now, various types of ncRNAs have been reported in plants like *Arabidopsis* [83], sugar beet [157], rice [155], wheat [23], tomato [12, 138], brassica [140], soybean [45], sorghum [127], ginseng [12, 15], pigeon pea [92], and *Brachypodium* [166]. Under high salinity and drought conditions, *Arabidopsis* Transacting Short Interfering RNA-Auxin Response Factor (tasiRNA-ARF) played a critical role in supporting the normal floral morphology in *Arabidopsis* [56]. Regulation of flower formation in pigeon pea is carried out by the interplay between Csa-lncRNA\_1231 and Csa-miRNA-156b through the expression of SPL-12

(SQUAMOSA PROMPTER BINDING PROTEIN-LIKE 12) [34]. Moreover, under salt stress, lncRNA973 upregulated its expression in cotton, and lncRNA 973-overexpressing *Arabidopsis* showed remarkable salt tolerance capacity [161]. In rice, the knockdown of a gene *OsDWARF4* through the RNAi promoted the development of shorter plants with enhanced photosynthetic capacity in lower leaves due to the erect leaf architecture of the RNAi plants [38]. Thus, small RNAs play a pivotal role in plant development, stress management, and crop improvement.

With the development of newer molecular biology techniques and bioinformatic tools, the involvement of ncRNAs or sRNAs in plant development and stress regulation has gained prominence. Sometimes, many identical ncRNAs play a pivotal role in plant development and stress tolerance [76]. Recently, it was found that the genetic transformation of ncRNAs can bring about phenotypic change [82, 92]. Finding out the ncRNA or sRNA-mediated developmental pattern and its interaction with stress regulatory mechanisms are essential to understanding plant stress biology and developmental strategies for crop improvement [98].

This review aims to understand the functional roles of sRNAs in the following three aspects: (1) plant development process (tissue patterning to lateral organ morphology); (2) use of RNAi technology in crop improvement to acquire agronomically desirable traits; and (3) understanding the sRNA-mediated stress regulatory network to deploy them judiciously to develop climate-resilient crops.

## Non-coding RNA and their classification

Out of 90% of eukaryotic transcribed RNAs, only 2% is translated into protein products [113, 119]. The rest of the untranslated transcribed RNAs represent ncRNAs, which are treated as transcriptional noise with poorly conserved sequences [113]. Later, high-throughput sequencing technology revealed that ncRNAs play crucial roles in transcription, translation, and epigenetic regulation [25, 117, 118, 134].

Based on molecular structure, plant ncRNAs have two types- linear ncRNAs and circular ncRNAs. Linear ncRNAs are further classified into housekeeping ncRNAs and regulatory ncRNAs. Fundamentally, the housekeeping ncRNAs are of four types, namely, tRNAs, snRNAs, rRNAs, and small nucleolar RNAs (sno RNAs). Basically, they possess cellular and ribosomal functions. On the other hand, based on molecular function, regulatory ncRNAs are broadly categorized into two types- sRNAs and long ncRNAs (lncRNAs) [70]. In plants, sRNAs include miRNA, heterochromatic small interfering RNAs (hc-siRNAs), natural antisense transcript-derived small interfering RNAs (nat-siRNAs), repeat-associated siRNAs (rasi-RNAs) and transacting siRNAs (tasiRNAs) [32, 63, 92]. On the basis of genomic location of their protein-coding genes, long non-coding RNAs are further divided into long intergenic ncRNAs, antisense ncRNAs (ancRNAs), intron ncRNAs, and sense ncRNAs (sncRNAs) (Fig. 1). All lncRNAs control transcriptional activity as *cis* or *trans* regulators [92, 138].

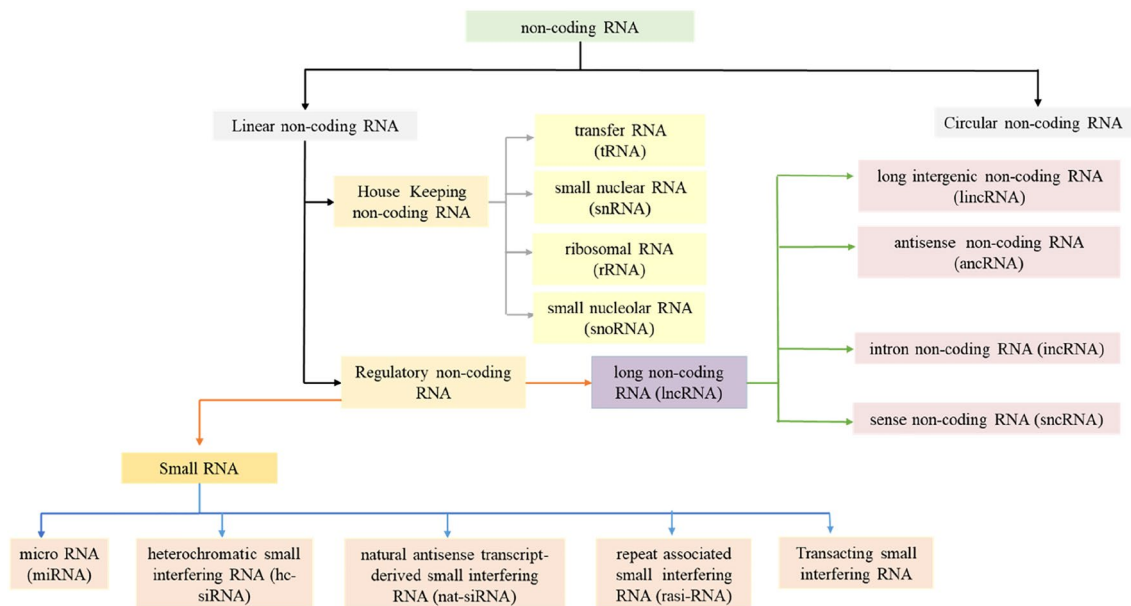


Fig.1 Classification of non-coding RNAs

## Small RNA: miRNA and siRNA

MicroRNAs and siRNAs are nearly similar in size but have different precursor structures, modes of action, and biogenesis [8, 62]. Developmentally, miRNA and siRNA are derived from long RNA precursors via the action of dicer-like ribonucleases [13, 50, 51, 57, 62, 71] and are involved in various gene repression mechanisms through ribonucleoprotein silencing complexes [62].

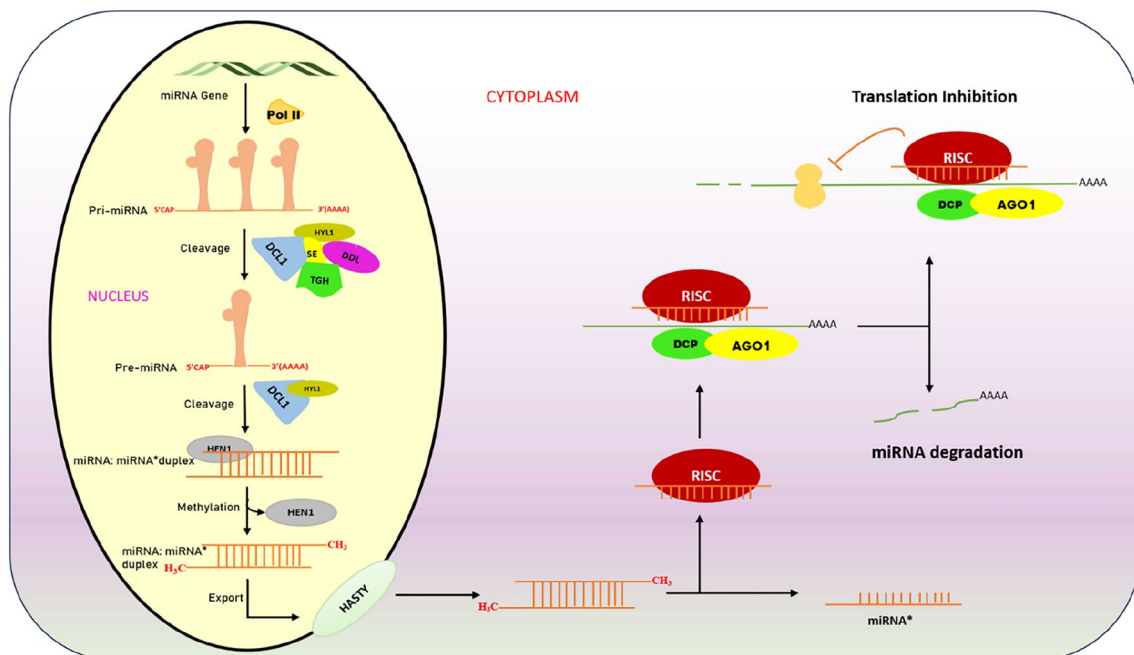
### Biogenesis of miRNA

Plant miRNAs (ncRNA molecules) consist of 19–25 nt and are considered under the class of small regulatory RNAs [59]. Intergenic genomic regions are the typical location of miRNA genes; however, sometimes, antisense or sense orientation RNA within a protein-coding gene intron are the sources of miRNAs [36]. Due to their clustered nature, miRNAs are often transcribed as long polycistronic RNAs [36].

In the plant nucleus, RNA polymerase II transcribes MIR genes into pri-miRNA (long primary transcripts) [10, 59]. They are capped at the 5'-end with modification and polyadenylated at the 3'-end [36, 109]. An RNase III-like enzyme, known as DICER-LIKE (DCL 1), cleaves the transcripts (pri-miRNAs) in two steps to form a hairpin-loop structure and a mature miRNA duplex (miRNA/miRNA\*) in the nucleus [10, 110, 114]. The 3'-end of this duplex is methylated by the conserved HUA enhancer1 (S-adenosyl-L-methionine dependent RNA methyl transferase) [104]. After duplex formation, it forms a complex with RNA-induced silencing complex (RISC) and AGO1 [5] (see box 1) protein. A part of the RISC complex helps to unwind the miRNA duplex [4]. A small RNA-degrading nuclease eschews one strand of the miRNA duplex. When the miRNA maturation process is over, its production is regulated either by site-specific cleavage of the miRNAs (requires high homology between miRNA and targeted mRNA) or by translational repression of miRNA (that stops the downstream expression of targeted product) (Fig. 2) [36, 127].

#### Box 1 Argonaute proteins

Argonaute (AGO) belongs to an evolutionary conserved family of proteins found in archaea, bacteria, fungi, plants, and animals. The RISE (the single-stranded small RNA and Argonaute protein complex), PAZ, MID, and PIWI are the most important functional domains of the Argonaute protein [57]. PAZ domain helps to bind miRNA duplex onto the AGO protein via a 2-nucleotide single-stranded overhang of the duplex. The H-fold structure of RNA confers endonucleolytic activity in the PIWI domain, which is responsible for small RNA-guided mRNA silencing [26]

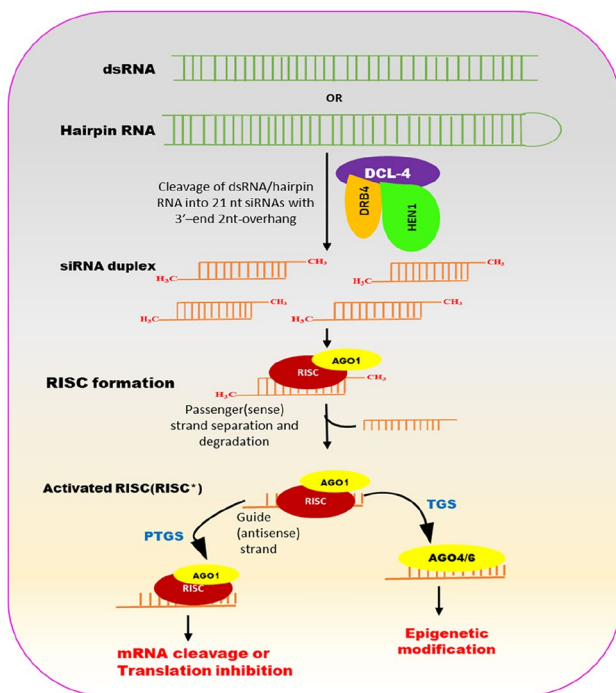


**Fig. 2** Micro RNA biogenesis and their regulations in the plant cell. The miRNAs undergo transcription by RNA pol II within the nucleus, resulting in the formation of primary miRNAs (pri-miRNA) that adopt a hairpin structure

## Biogenesis of siRNA

Given differences in function and biogenesis, the siRNAs are categorized into trans-acting siRNAs (tasiRNA), natural antisense siRNAs (nat-siRNAs), and heterochromatic siRNAs (hc-siRNA) [134]. TasiRNAs share a common regulatory mechanism with miRNAs. However, hc-siRNAs act in the cis region of their source. The nat-siRNAs are classified into cis and trans configurations [134, 167]. Long dsRNAs or short hairpin RNAs (snRNA) start the process of PTGS (Post Transcriptional Gene Silencing) or RNAi as they complement the target gene sequence. The RISC containing AGO, DCL enzyme, and dsRNA act as main precursor molecules for the siRNA synthesis [167]. The dicer enzyme truncates the dsRNA to a shorter form with 5' phosphorylated end and 3' overhangs(2nt) [62]. The siRNA-induced silencing complex (siRISC) degrades the sense strand of siRNA. After degradation, the siRISC complex binds to an antisense strand of siRNA, along with AGO and other effector proteins, to degrade the target mRNA [62, 79] (Fig. 3).

Formation of tasiRNAs depends on SUPPRESSOR OF GENE SILENCING 3 (SGS3), RNA-dependent PNA polymerase 6 (RDR6) and DCL4 [18, 43, 116]. In *Arabidopsis*, four types of DCLs are found, of which DCL4 and DCL2 regulate siRNA biogenesis (20–22 nt) [19]. DCL1



**Fig. 3** Plant siRNA biogenesis. The conversion of double-stranded RNA into siRNA is facilitated by DCL, HEN, and DRB. Subsequently, the RISC-AGO complex directs the specific strands of the siRNA duplex toward PTGS (Post Transcription Gene Silencing) or TGS (Transcriptional Gene Silencing)

is involved in the processing of miRNA (21 nt long) [10], whereas DCL3 assists in the formation of heterochromatic siRNAs (hcsiRNAs, 24 nt long repeats) [149]. DCL1 and DCL2 contribute to nat-siRNA biogenesis along with SGS3 and RDR6 [18]. Once produced, siRNAs with some DNA and histone-modifying proteins, like the cytosine methyltransferase and chromomethylase 3, form a silent (transcriptionally inactive) chromatin state.

## Movement of small RNAs

Cell-to-cell communication is the basis of multicellularity and tissue organization. To maintain cytoplasmic connection, plant cells allow intercellular interaction via plasmodesmata, i.e., ‘symplasm’ [95]. In plants, along with metabolites, peptides, proteins, and hormones, some RNAs (messenger and small RNAs) are also translocated from cell to cell via the symplast (by plasmodesmata and nanoscale channels of cell wall) [132]. Both long and short-distance RNA movements are reported in different plant organs. Moreover, some recent studies reported that RNA interchanges between various plants and colonizing organisms (microbes or parasites) take place via exosomes or selected vesicles [95]. More than a decade ago, it was observed that transgene silencing initiated in a single leaf or root and subsequently transmits systematically throughout the whole plant. Hence, it is evident that small RNA can traverse short (plasmodesmata) and long distances (vasculature) [29, 97].

An experiment with wild-type young shoots and rootstock (deficient in *dcl2/3/4* siRNA biogenesis) demonstrated that endogenous siRNAs (23–24 nt) can travel from shoot to root and control the PTGS process [73, 100]. The miRNA can also travel through phloem assisted by various favorable physiological cues. Under sulfate, phosphate, and copper deficiencies, some miRNA species (miR395, miR398, and miR399) increase their level remarkably in phloem sap. In *Lotus japonicus*, miR211 traveled from shoot to root to control the availability of the symbiosis suppressor TOO MUCH LOVE (TML) to regulate healthy roots [44, 133]. Such mobility of small RNA species is really intriguing, particularly their roles in multiple stress responses, which might have a correlation with the magnitude of plant stress levels.

## Role of small RNAs in the plant development

Plant development is an ‘umbrella term,’ which denotes the growth and differentiation of a plant during its entire lifespan, i.e., from germination to senescence. Some sRNAs play a central role in the developmental pathway through their participation in different signaling mechanisms (Table 1).

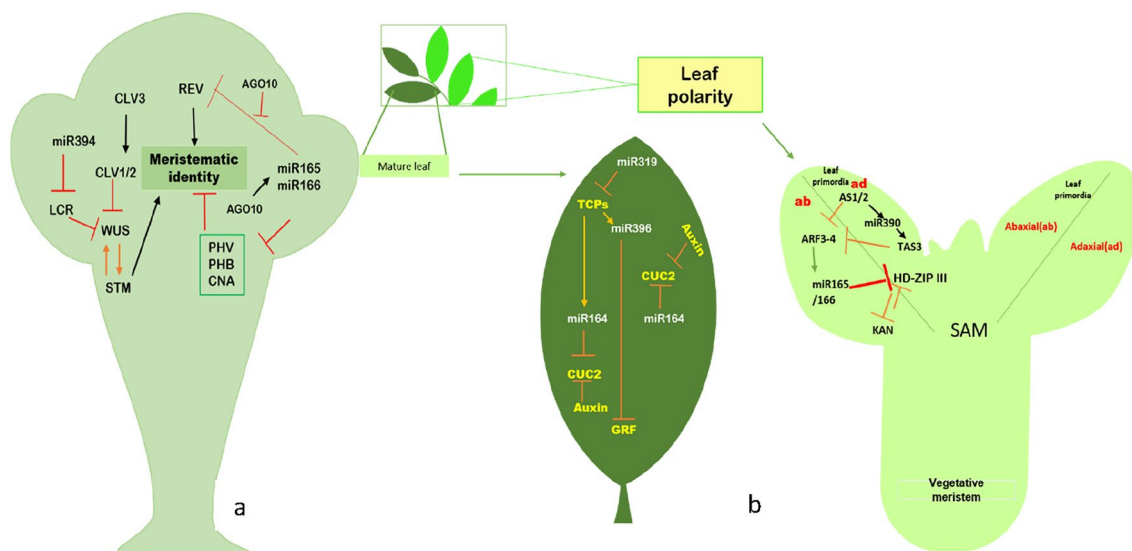
**Table 1** List of miRNAs associated with the plant development

Plants	Micro RNAs	Targets	Functions	References
<i>Arabidopsis</i> , maize	miR156	SPL family	Induction of flowering;	[30, 31, 33]
<i>Arabidopsis</i> , maize, <i>S. tuberosum</i>	miR172	AP2 family	Identity of flower meristem; flower patterning; development of carpel and stamen in maize; tuberization in <i>Solanum tuberosum</i>	[33, 129, 141]
<i>Arabidopsis</i>	miR159	MYB33	Development of Anther, silique, and seed	[1, 4, 33]
<i>Arabidopsis</i> , <i>Solanum</i> , <i>Oryza</i>	miR164	CUC	Identity of meristem boundary, formation of auxiliary meristem, leaf serration	[22, 33, 54]
<i>Arabidopsis</i>	miR167	ARF6 and ARF8	Male organ development	[33, 143]
<i>Arabidopsis</i>	miR165/166	HD-ZIP III	Adaxial identity of leaves, Maintenance of meristematic cells, Identity of procambium, lateral root growth	[33, 93, 105]
<i>Arabidopsis</i>	miR393	TIR1 and AFB	Auxin homeostasis	[33, 112]
<i>Arabidopsis</i>	miR390	TAS3	ARF repression via tasiRNA biogenesis, regulation of miR165/166	[33, 101]
<i>Arabidopsis</i>	miR319	TCP family	Control of cell growth and proliferation (during development); leaf and petal shape	[33, 107]
<i>Arabidopsis</i>	miR394	LCR	Suppression of meristem identity via WUS downregulation	[33, 66]
<i>Arabidopsis</i> , <i>Medicago</i> , and <i>Oryza</i>	miR396	GRF	Leaf cell proliferation	[33, 84]

## Meristem development

Shoot apical meristem (SAM), a specially organized structure, is the predominant meristem in a plant. The dividing cells of SAM are evolved into plant leaves [92]. In SAM, the development of meristematic cells are regulated by the STM-WUS-CLV pathway [41]. Here, various miRNAs interplay to regulate the development of SAM. In the L1 (protoderm) layer of the SAM, miR394 controls the expression of WUSCHEL (WUS), and later on, it moves through the

organizing center (OC) of the SAM to inhibit the expression of LCR or LEAF CURLING RESPONSIVENESS (LCR) [66]—a direct inhibitor of WUS [124]. The process of SAM-related development of shoot apex is carried out by regulation of class III HOMEODOMAIN LEUCINE ZIPPER (HD-ZIP III), PHABULOSA (PHB)/ATHB14, PHAVOLUTA (PHV)/ATHB9, INTERFASCICULAR FIBERLESS/REVOLUTA (IFL1/REV), INCURVATA4/CORONA/ATHB15, and ATHB8 specifically targeted by both miR165 and miR166 species of miRNAs [168] (Fig. 4a).



**Fig. 4** Role of miRNA in the plant development. **a** Regulation of meristem identity. The expression of WUSCHEL(WUS) is confined to the organizing center solely through two parallel mechanisms, namely the CLV pathway and the miR394-mediated regulation. **b**

Regulation of leaf shape, polarity and Shoot Apical Meristem. The adaxial and abaxial surfaces are determined by HD-ZIP III. [ab-abaxial, ad-adaxial] Positive regulation → Negative regulation —

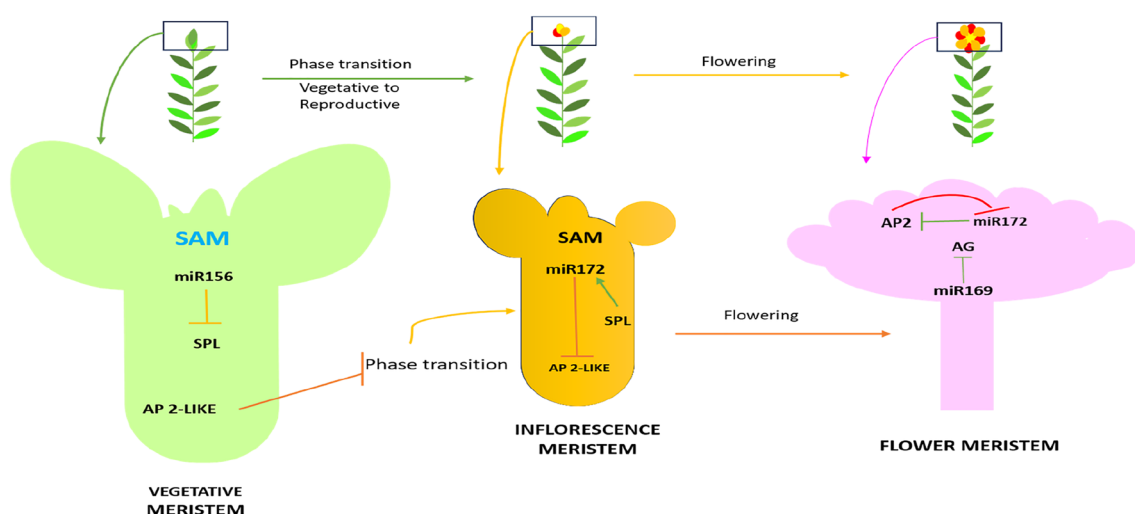
## Development of leaf

A set of meristematic cells in the peripheral area of the shoot apical meristem (SAM) are responsible for the development of leaves [96]. The leaf polarity (adaxial or upper surface and abaxial or lower surface) is determined by two HD-ZIP III genes, PHABULOSA (PHB) and PHAVOLUTA (PHV) [96] (Fig. 4b). The expression of HD-ZIP III is negatively regulated by miRNA165/166, which is expressed abaxially [64]. A maize mutant (rolled leaf 1, *rdl1*) (a *Zea mays* HD ZIP III homolog) and a gain-of-function *Arabidopsis* mutant (*phb-1d*) showed abnormality in the development of leaf polarity due to a mutation at the miR165/166 binding site of RDL1 and PHB [60, 103]. Other miRNAs also play an important role in the leaf lamina development. In *Arabidopsis*, leaf serration occurs due to auxin and CUC2 interaction [136] (Fig. 4b). The miR164 controls the CUC2 and performs a pivotal role in the formation of compound leaves [16]. In tomato and *Arabidopsis*, the mutation in the miR164 binding site forms a smooth leaf margin [12, 104]. The TCP gene exerts an indirect regulatory influence on the expression of CUC2 by inhibiting miR164 [67]. The formation of leaf shape is governed by GROWTH-REGULATING FACTORS (GRFs)—a cohort of transcription factors closely linked to cell division and cell elongation. Overexpression and loss of function study of GRF 1, 2, and 3 showed the development of large and small leaves [55, 65]. The miR396 regulates the expression of GRF genes. In the distal region of developing leaf blades of *Arabidopsis*, miR396 regulates the activity of GRF and helps to continue cell proliferation in the proximal region [121]. In the developing leaf of a mature plant, the

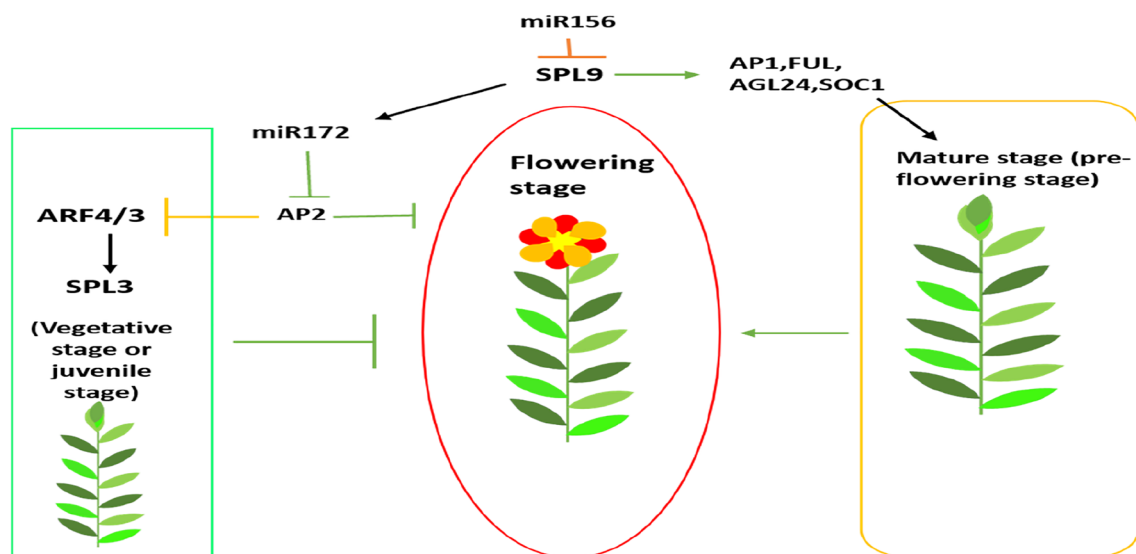
amount of GRF is diminished, and the miR396 amount is increased [121]. Notably, the regulations of bidirectional, acropetal, and basipetal growth of different leaves are directed through the miR396-GRF pathway [48]. In *Arabidopsis* leaves, miR393 controls the expression of the TIR1/AFB2 (auxin receptor) involved in auxin-related development [122]. In rice, the formation of the enlarged flag leaf is correlated with overexpression of miR393, which targets related TIR1 homolog during auxin signaling [14, 80].

## Flower development and patterning

Apart from various networks of different types of genes, many of the sRNAs are also engaged in floral patterning and development. However, floral transition, i.e., shifting from the vegetative to the reproductive phase, happens under the cooperation of some miRNAs and their target genes [92] (Figs. 5 and 6). In *Arabidopsis*, the acceleration of flowering is achieved through translational inhibition of the floral homeotic gene APETALA2 (AP2) by the overexpression of miR172 in shoot apical meristem (SAM) [26, 58, 141] (Fig. 5). The miR172 is a crucial factor in flower patterning, accumulates at the center of flower primordia where the class C gene AGAMOUS (AG) is expressed. This accumulation of miR172 leads to AP2 suppression, thereby inhibiting the co-expression of the A and C homeotic genes, delimiting the petal and stamen development [164]. Furthermore, AP2 functions to downregulate miR172, establishing a vital negative feedback loop that is essential for the precise determination of organ identity [27, 153]. The intricacy of this network is further exemplified by a recent investigation, which has revealed that TARGET OF EAT 3 (TOE3) plays a



**Fig. 5** Roles of different miRNAs in phase transition (vegetative to reproductive). The AP2-like gene inhibits the phase transition, whereas SPL promotes flowering through the activation of miR172



**Fig. 6** Involvement of different miRNAs during phase transition (vegetative to flowering stage via mature stage)

decisive role during the signaling interplay between miR156 and miR172 [61, 142]. Flowers with optimum organ size and preserved flower meristem identity were correlated with overexpressed transcripts of TOE3 (resistant to miR172) [51, 61]. The study offers further substantiation regarding the involvement of SPL3, which facilitates the activation of both TOE3 and its repressor miR172. This interaction among these three components (SPL3, TOE3, and miR172) establishes a negative feedback loop, which effectively governs the precise localization of TOE3 [61]. SPL9, a potent transcriptional activator of miR172, exerts precise and direct regulation over the expression of *AP1*, *FUL*, *AGL24*, and *SOC1* through its binding to their individual promoters [135] (Fig. 6). The BLIND (BL) in *Petunia* and the FISTULATA (FIS) in *Antirrhinum* encode miR169, which regulate the expression of AG homologs [24, 92]. Thus, both miR172 and miR169 decisively regulate the expression of the ABC gene. Remarkably, the presence of a detectable miR172-binding site can be observed in barley *AP2* homolog CLEISTOGAMY1 (CLY1) [94].

Furthermore, it has been demonstrated that miR172 functions as a mobile element capable of diffusing over considerable distances in potato [102]. In potato tuberization, it is possible to augment the process (long-distance travel) through grafting with miR172 expression lines [102]. Additionally, this finding serves as an additional justification for the potential application of small RNAs to achieve targeted biotechnological objectives. The above findings validate the long-distance mobility of miRNA in plants during signal transmission.

After the successful establishment of floral patterns in an organized manner, floral primordia also form a complex

structure and lead to the development of a complete flower under the cooperative action of several miRNAs and their target genes. Crosstalk between auxin and some miRNAs, such as ARF6, ARF8, and miR167, contribute to the formation of male flowers [143]. Additionally, the expression of TIR1 and AUXIN SIGNALING F-BOX (AFG) genes are regulated by miR393 during flower development [112]. Moreover, anther and silique fruit formation are determined by miR159 via MYB33 [1, 4]. Double-mutant study of miR159 binding site (*miR159a* and *miR159b*) in MYB33 showed impaired fertility, development of small siliques, retarded anther formation, and development of smaller seeds [1, 4, 120].

Besides being important regulators of floral organ identity, miR172 (responsible for the adult phase) and miR156 (responsible for the juvenile phase) are also associated with the vegetative to reproductive phase transition. Delay and induction of flowering were found to be controlled by overexpression of miR156 and miR172 [6, 148]. In monocot and dicot plants, AP2-LIKE genes [6] inhibit flowering by convergent action of siRNA [106] with other repressors during long-day conditions [72]. AP2-LIKE transcript is destructed by miR172 (promoted by the SPL family) [154], and the miR156 blocks the SPL activity in the juvenile phase [144], ultimately inhibiting the flowering. Contrarily, in adult plants, miR156 transcripts decrease and initiate the biogenesis of SPL protein to activate miR172 transcripts and hasten flowering. Therefore, the miR172-miR156 complex, along with their respective target genes, perhaps evolved to control flower patterning and phase transition (Figs. 5 and 6). The anatomical (cellular) transition from vegetative to reproductive phase, adaxial to abaxial form, and sepal to



petal transformation are crucially linked to the participation of certain sRNAs.

The sRNAs perform diverse functions ranging from regulation of essential determinants of meristem identity, leaf polarity, and flowering process throughout the course of plant development. Mutations during transcription and processing of small RNAs produce pleiotropic effects across plant developmental stages, right from plant dimensions, leaf and flower morphology, as well as the timing of flowering. This underscores the significance of microRNAs in coordinating various phases of plant development.

## Role of small RNAs in abiotic stress management

Plants, in their entire life period, constantly struggle to adjust to various environmental stresses that adversely affect their natural growth and development. Unfavorable conditions, especially abiotic stresses (drought, heat, cold, salinity), are well documented that severely impact plant productivity

[162, 168]. In response to such abiotic stress conditions, a diverse array of sRNA and ncRNAs differentially express as a part of adaptive strategies (Table 2).

## Heat stress

In the last few decades, there has been mounting evidence suggesting the loss of crop productivity due to drastic climate change, particularly due to heat stress [85]. By the end of the twentieth century, the loss of global wheat and maize productivity is expected to reach 5.5% and 3.8%, respectively, due to a 0.13° C temperature rise [169]. Plants are equipped with metabolic machinery to combat heat stress. There are several factors, like heat shock proteins (HSPs), heat shock transcription factor (HSFs), ROS scavenging enzymes, and small RNAs, that work cooperatively to offer thermotolerance [106]. Indeed, several sRNAs are found to be associated with heat stress mitigation and thereby offer thermotolerance. Several miRNA families (mi156/miR172, miR159/miR319, miR160/miR393, and miR398) function

**Table 2** List of miRNAs and siRNAs associated with plant abiotic stress responses

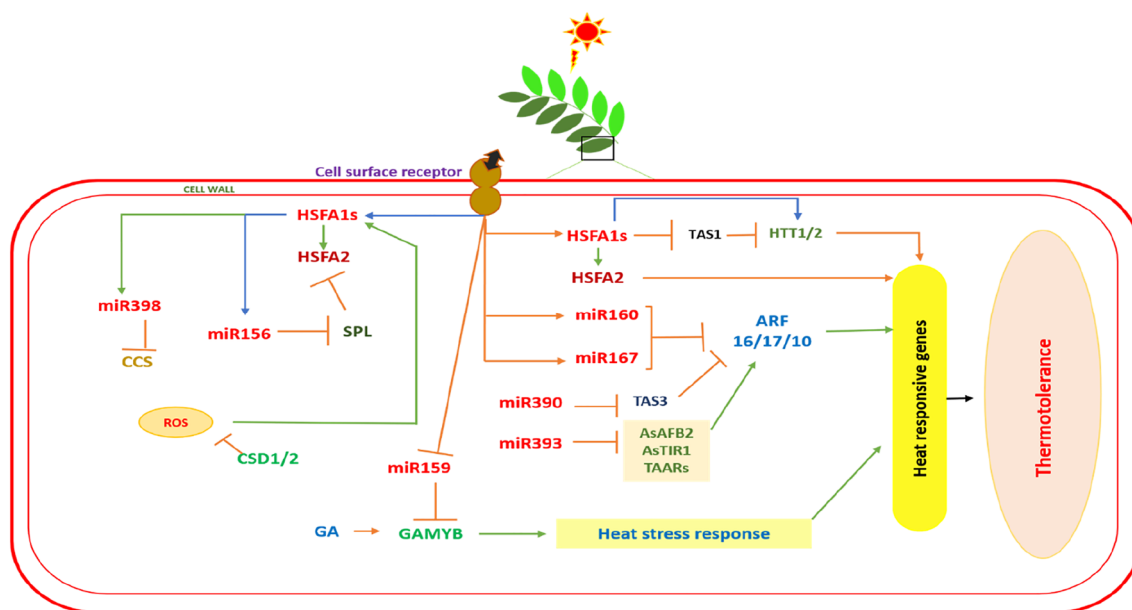
Plants	miRNAs or siRNAs	Targets	Abiotic stresses	References
Wheat	miR159	TaGAMYB	Heat	[150]
<i>Arabidopsis</i>	miR398	Copper/zinc superoxide dismutase (CSD1 and CSD2)	Heat	[46]
<i>Arabidopsis</i>	miR160	AUXIN RESPONSE FACTOR10 (ARF10), ARF16, and ARF17	Heat	[81]
Rice	miR394	F-box protein	Drought	[11]
Maize	miR169	Nuclear transcription factor	Drought	[89]
Chickpea	miR408	DREB transcription factor	Drought	[49]
<i>Sorghum bicolor</i>	miR167	Transcription factor ARF8	Drought	[52]
<i>Sorghum bicolor</i>	miR393	TIR1 and AFB2	Drought	[52]
Wheat	miR398	Cu/Zn superoxide dismutase (CDS1 and CDS2) and copper proteins COX5b	Drought	[3]
Wheat	miR160	Auxin response factors (ARFs)	Drought	[3]
<i>Arabidopsis</i> , Rice, Cowpea, Maize, Peach, Tobacco, Wheat	miR396	Growth-regulating factor (GRF)	Drought	[3]
<i>T. dicoccoides</i> , <i>M. truncatula</i> , Barley, Wheat	miR166	Homeodomainleucine zipper (HD-Zip III) transcription factors	Drought	[3]
<i>Arabidopsis</i>	miR394	LCR (Leaf Curling Responsiveness)	Cold	[125]
Cassava	siARF1, siARF3	ARF	Cold	[145]
Rice	miR156	OsSPL3—SBP-box gene family member	Cold	[165]
Peach	miR393	TIR1, AFB2, AFB3	Cold	[9]
Citrus limon	miR396b	1-aminocyclopropane-1-carboxylic acid oxidase (ACO)	Cold	[160]
<i>Arabidopsis</i>	miR408	CSD1, CSD2, GST-U25, CCS1 and SAP12	Cold	[90]
Rice	miR319	OsPCF6 and OsTCP2	Cold	[137, 152]
Creeping bent grass	miR528	Ascorbic acid oxidase and copper binding protein 1	Salt	[156]
Soybean	miR172a	Salt suppressed AP2 domain-containing gene (SSAC)	Salt	[108]

at the center of the gene regulatory network that play critical roles in coordinating heat stress tolerance by adaptive strategies towards thermal stress [169] (Fig. 7). The SQUAMOSA PROMOTER-BINDING PROTEIN-LIKE (SPL), the target of miR156, together regulate the phase transition (juvenile to adult and vegetative to reproductive) [91]. The miR156 also controls the high temperature-induced stress conditions in plants [103]. Under heat stress (37°–44°), miR156 isoform overaccumulates and regulates the expression of heat stress-responsive genes in *Arabidopsis*. The miR156 was reported to be responsible for heat stress memory, and it helps plants retain thermotolerance even after returning to favorable growing temperatures [69]. In this context, it is interesting to note that plants exposed to previous heat stress conditions retain the experience as “heat stress memory,” which they recall during subsequent exposures to heat stress. Heat stress memory can be increased through the inhibition of SPL2 by miR156. This entire phenomenon is controlled by the HSFA2 cascade, which is associated with HEAT STRESS-ASSOCIATED32 (HSA32) and ROF1 [126]. On the other side, miR172 targets the AP2 family genes (AP2, TOE 1, 2, and 3; SCHNARCHZAPFEN or SNZ; and SCHLAFMUTZE or SMZ) and acts as a positive regulator of phase transition in plant [91]. Under optimal growth conditions, the development of flowers takes place in a thermosensory manner by the action of miR172 [70]. Hence, the miR172-AP2 module plays a critical role in heat stress response [115].

The miR159 and miR319 regulate the male fertility and leaf growth [2]. Some members of GIBBERELLIC ACID MYB (GAMYB) are regulated by miR159 and support flower formation and male fertility. Under heat stress, miRNA levels lower while CsGAMYB1 and CsMYB29 (cucumber) levels increase, which underlines their involvement in heat stress response [77]. On the other hand, in *Gossypium hirsutum*, under extreme heat conditions, overexpressed miR160 blocks ARF10 and ARF17, thereby making the plant susceptible to heat stress, resulting in indehiscent anthers, which reduces crop productivity [35, 40].

The CSD, a significant ROS-scavenging enzyme, influences the expression of SODs (like Fe-SOD, Cu/Zn-SOD, and Mn-SOD) under heat stress. In *Arabidopsis*, in response to heat stress, the miR398 gets upregulated to suppress its target genes (CSD1, CSD2, and Copper Chaperone for SOD) [46].

A small RNA species, Osa-miR5144, in rice, is also associated with heat stress adaptation. This RNA manipulates the expression of *OsPDIL1;1* (protein disulfide isomerase) responsible for protein disulfide bond formation [147]. MicroRNA400 is the primary transcript that undergoes heat stress responsive alternative splicing of the intron, causing lower availability of mature miR400. Therefore, in a heat stress resistance plant, miR400 acts as a negative regulator [151]. In light of crop productivity, it is noteworthy that a host of heat shock proteins, HSFs, miRNAs, hormones, and even alternative splicing collectively offer effective thermal protection to the crop plant (Fig. 7).



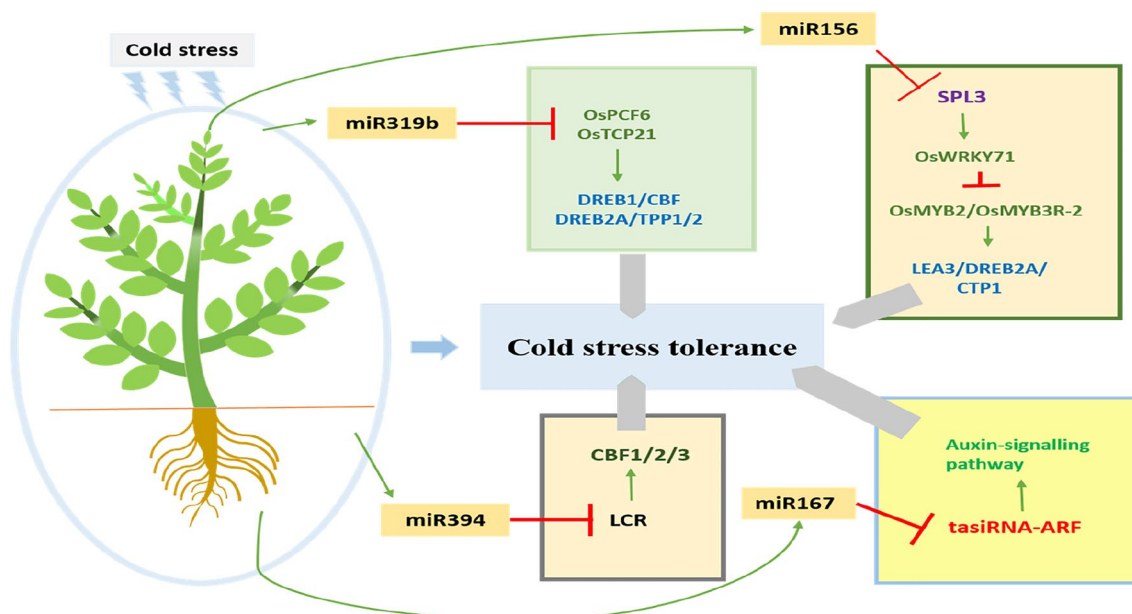
**Fig. 7** Small RNA regulation during heat stress. The miR160, miR167, miR159, miR156, and miR398 play predominant roles in heat stress response

### Cold stress

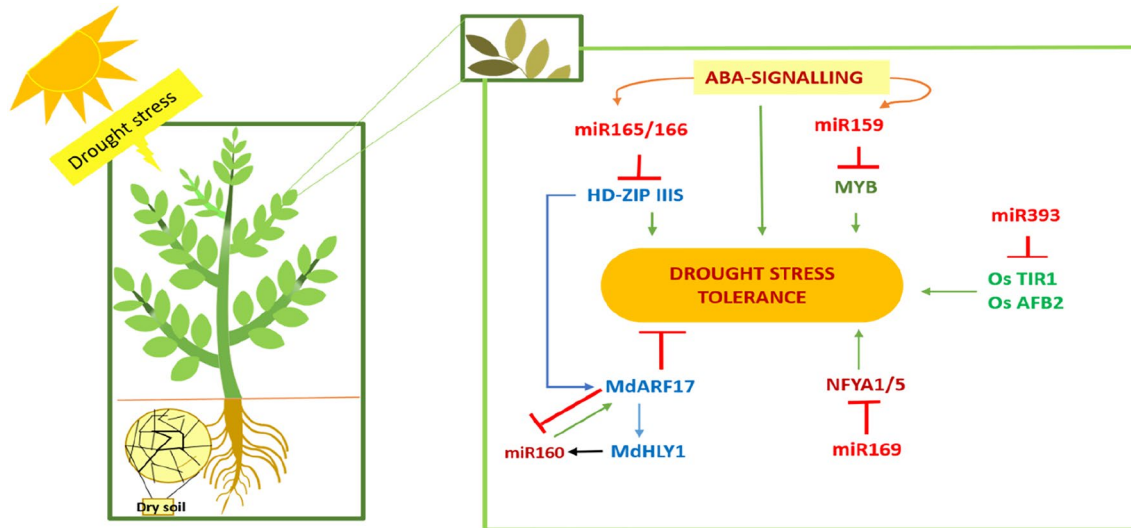
Cold stress poses significant challenges to the growth and development of plants, as it affects their physiology and metabolism by altering their cellular homeostasis [92]. Here, the reliable ABA-independent pathway rescues plants during cold stress by activating ICE or Inducer of CBF expression. This pathway further leads to the activation of CBF/DREB1, a downstream transcription factor, by ICE. Eventually, CBF/DREB1 attaches to CRT (C-repeat elements) or LTRE (Low Temperature-Response Element), resulting in the upregulation of COR or cold-responsive genes [47, 68]. Among diverse miRNAs, Osa-miR319b upregulates under cold stress in rice. However, the over-expression of Osa-miR319b simultaneously downregulates *Ospcf6* and *Ostcp21*, upregulates cold-stress responsive genes, including *Bdreb1/CBF* (Dehydration Responsive Element Binding Protein/C-repeat Binding Factor), *DREB2A*, and *TPP1/2* [7]. Additionally, *OsSPL3*, which is targeted by *OsmiR156*, exerts a positive control on *OsWRKY71*. Contrarily, both *OsMYB2* and *OsMYB3R-2* are negatively regulated by *OsWRKY71*. Consequently, this regulation leads the downstream activation of various stress-responsive genes such as *OsLEA3*, *OsDREB24*, and *OsCTP1* [165]. In the case of wheat, both *tasiRNA-ARF* and *miR167* play a critical role in governing the auxin-signaling pathway and facilitate the development of the cold stress response [130] (Fig. 8).

### Drought stress

Drought stress or water deficit condition poses a lethal threat to crop survival. It is interesting to note that changes in small RNA population correlate with severe dehydration, extreme drought, or even water deficit conditions [128]. The following case studies highlight these issues. *Arabidopsis* displayed upregulation of *miR393*, *miR397b*, and *miR402* and downregulation of *miR319c* and *miR389a* in response to dehydration stress [128]. Rice seedlings subjected to drought stress upregulation of 16 miRNAs and downregulation of 17 miRNAs [158]. Maize leaves showed upregulation of 8 miRNAs and downregulation of 13 miRNAs, whereas root displayed upregulation of 7 miRNAs and downregulation of another seven miRNAs under drought stress conditions [87]. Notably, *miR171*, *156*, *160*, *162*, and *164* species were found to downregulate the expression of their respective target genes during drought stress, which indicates their valuable roles. The intriguing study by Shen et al. [123] highlights that *Mdm-miR160* moves from the scion to the rootstock, contributing to drought adaptation and root formation in apple. The *MIR160* plays a vital role in promoting the activation of *MdARF17* through the formation of a positive feedback loop, and it specifically binds to the promoter region of *MdHLY1* [123]. In *Arabidopsis*, the *miR165/166*-mediated regulation of HD ZIP IIIs facilitates ABA signaling, which is crucial for drought adaptation. Moreover, HD-ZIP IIIs activate ARF, the target of *miR16*. This cooperative interaction between *miR160* and *miR165/166* enables plants to respond to and tolerate drought stress [86]. On the other hand, the



**Fig. 8** Roles of different miRNAs in cold stress tolerance. The miR319, miR156, miR167, and miR394 regulate the signaling events in plants with their targets



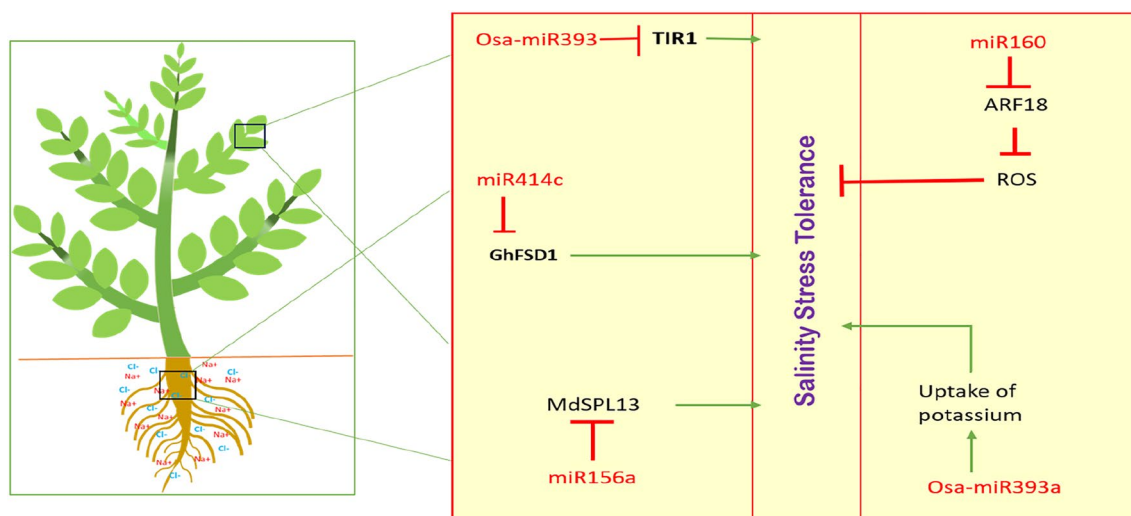
**Fig. 9** Roles of different miRNAs in drought stress tolerance. The miR159, miR169, miR393, miR160, and miR165/166 play vital roles in drought stress mitigation via ABA and auxin-mediated signaling

ABA-dependent response to drought stress involves the miR159-MYB and miR169-NFYA components [86]. In *Arabidopsis*, miR159 modulates the cleavage and regulation of MYB33 and MYB101 during the germination phase, which assists in responding to drought stress and the accumulation of ABA [121]. Interestingly, the ABA-dependent pathway suppresses the expression of miR169 in the face of impending drought stress [92]. Indeed, the sensitivity to drought stress in *Arabidopsis* came to light through the study of miR169a expression and knockout experiments involving *nfya5*. However, the overexpression of *NFYA5* promotes better adaptability to drought stress [78]. Similar patterns can be observed in *Brassica napus* and soybean, where

the targets of miR169, namely NF- $\gamma$ A $\delta$ , AtNFYA1, and AtNFYA5, inhibit the production of stress-induced genes and exhibit a negative response to drought conditions [75, 154] (Fig. 9).

### Salinity

Salinity or salt stress, akin to other abiotic stresses, impedes the natural growth and reproductive processes of plants. In this discourse, we shall delve into the significance of plant miRNAs and their respective target genes in alleviating the effects of salinity stress. In peanuts, similar to drought stress, the miR160 and its target gene ARF



**Fig. 10** Involvement of miRNAs in salinity stress tolerance. The miR160, miR393, and miR414 determine tolerance to salinity stress

exhibit heightened expression in response to salt stress. In saline conditions, the ARF18 pathway, triggered by the overexpression of miR160, facilitates seedling growth and neutralizes the impact of ROS [131]. Furthermore, certain plants demonstrate distinct reactions or promotion effects toward salt tolerance by different or identical miRNAs that belong to the same family. For instance, in rice and *Arabidopsis*, the overexpression of Osa-miR393 results in diminished salt tolerance [42, 47, 146], whereas overexpression of the resistant form, MTIR1, of miR393 leads to enhanced salt tolerance [28]. In cotton, both miR414c and its target gene GhFSD1 (Iron Superoxide dismutase 1) contribute to salt tolerance. The overexpression study of miR414c illustrates a reduction in GhFSD1 expression, making it susceptible to salinity stress by regulating ROS metabolism [139] (Fig. 10).

### Impact of small RNAs for the establishment of climate-resilient crops

Recent reports indicate that agro-climatic systems are becoming increasingly vulnerable to warming climatic conditions and changing precipitation patterns, with an expected impact on food security [53]. Various environmental stresses, like drought, soil contamination, rising temperatures, UV radiation, and atmospheric CO<sub>2</sub> and O<sub>3</sub> levels, pose a challenge to developing climate-resilient crops to meet the growing demand for food and feed. In the post-genomic era, biotechnological advancements provided a foundation for sustainable agriculture and increased crop flexibility in the face of climate change. To tackle these environmental challenges, breeding methods are combined with modern biotechnological tools to design stress-tolerant crops while maintaining high yields. The miRNAs, which play a crucial role in plant stress tolerance and environmental adaptation, promise immense potential for crop improvement [21]. The utilization of modern computational tools, databases, and high-throughput sequencing has contributed significantly to identifying numerous mRNAs that respond to single or multiple stress exposures [25]. Despite recent advancements in understanding the effects of plant miRNAs on growth, development, and stress responses, it is still limited for developing resilient crops that can thrive in challenging climatic conditions.

Exciting advancements have been made in the utilization of sRNAs to improve agronomic traits and bolster resistance to challenging environments. These small molecules play a crucial role in orchestrating the regulation of target genes to combat stress conditions [160]. Thanks to recent breakthroughs in high-throughput sequencing technology and bioinformatics, characterizing small RNAs and

their corresponding targets has become more accessible than ever before. The techniques of overexpression and knockdown are gaining popularity as powerful tools to introduce functional improvements and to investigate the loss of specific functions in transgenic plants [37]. Till now, a group of transgenic plants with altered miRNAs has been designed to understand their response to abiotic stresses.

In *Arabidopsis thaliana*, the overexpression vector containing pre-miR408 was utilized to generate transformants exhibiting superior qualities, as compared to control plants, such as the absence of chlorosis, wilting, and drying. The study on overexpression of miR408 demonstrated reduced expression of the target gene Plantacyanin, whereas genes Rd17 and Rd29, along with DREB1/2A (a transcription factor of Rd17 and Rd29), revealed enhancement in transgenic plants, which mediates a positive response to drought stress [49]. The overexpression of miR408 in *Cicer arietinum* improved drought tolerance. The transgenic plant *Agrostis stolonifera*, harbouring the pre-miR393a of *O. sativa*, displayed stronger resilience to salinity (at 250 mM for 10 days) and heat (at 40 °C Day/35 °C night, 13 days), suggesting miR393 would be an excellent candidate to confer multi-stress tolerance [163]. The utilization of miR172 facilitated the development of transgenic plants with enhanced adaptability under high salt and water deficit conditions [67]. The overexpression of *Glycine max*-miR172 in transgenic *Arabidopsis* led to an increase in germination rate, greater number of green cotyledons, and reduced leaf water loss. Glyma o1g39520 (AP2/ERF), identified as the predicted target of this miRNA in *Arabidopsis*, acted as a regulatory component responsible for improved tolerance capacity [77]. Overexpression of miRNA genes helps to achieve cold tolerance in *O. sativa* [113]. Seedlings that were genetically modified to overexpress Osa-miR319b were subjected to 4 °C for 7 days, followed by a recovery period of 10 days. It was observed that the transgenic plants showed a better recovery rate (up to 90%) compared to the mere 30% recovery in wild-type plants. In support of these findings, gene expression profiles of two predicted targets, *OsPCF6* and *OsTCP21*, were carried out, which indicated that these genes were inhibited by low temperatures, with wild-type plants displaying notable induction [137]. Another experiment conducted by Zhang et al. [158] involved the overexpression of miR396b from *Poncirus trifoliata* in Citrus lemon to enhance cold tolerance. Exposure of four-month-old transgenic and wild-type plants to cold (−2 °C) for 12 h resulted in a higher accumulation of polyamines, reduced level of ROS, decreased ACO transcripts, and lowered ethylene content. These findings can be hypothesized as potential factors contributing to the successful recovery and growth of these plants under cold stress.

Currently, strategies involving the overexpression of small RNAs are being explored globally to develop climate-resilient plants. However, there is a growing trend for the knock-out approach, specifically through the short tandem target mimic (STTM) method, to achieve the same purpose. This approach results in the loss-of-function of identified miRNA, which acts as a negative regulator. Zhang et al. [159] demonstrated that miR166 knock-out lines (STTM166) showed reduced stomatal conductance and transpiration rate, thereby ensuring better photosynthetic efficiency. Additionally, the miRNA's major target, *OsHB4*, was identified as a potential factor in improving drought tolerance. The study concluded that manipulating miRNA can lead to developmental changes, such as leaf rolling and reduction in xylem diameter, which mimic the response of plants under water deficit conditions. Various studies are being conducted to deploy miRNAs in engineering crops with the aim to withstand multiple stress conditions. The emerging global research trends in miRNA underline its emerging significance in developing climate-resilient crops through targeted overexpression of concerned genes and their miRNAs.

## Conclusion

Significant progress has been made in the study of plant sRNAs in recent years, establishing them as essential regulators of almost every aspect of the plant's life, including growth, development, and sensitivity to environmental stimuli. Recombinant-DNA-based crop engineering generally targets specific genes and proteins of agro-economic traits to improve crop productivity with stress tolerance. This research trend is supported by the availability of databases and molecular tools dedicated to miRNA-based research. Scientists have discovered a large number of miRNAs that are crucial for plants' responses to a variety of environmental challenges through the use of sRNAs and 'degradome sequencing' techniques and in silico biology. The ability of these miRNAs to target particular genes has been effectively predicted and increasingly explored.

Recent research suggests that plant miRNAs can be valuable targets for genetic engineering. The aim is to enhance stress tolerance in crop plants by manipulating miRNA expression through methods like overexpression or knock-out techniques, depending on their regulatory role. Despite limitations and the need for more research, early attempts in miRNA-based genetic engineering demonstrate their immense potential for developing climate-resilient crops. Furthermore, plant miRNAs are also being acknowledged as useful tools for genome editing, although further investigation is needed in this area.

Understanding the complexity of plant sRNAs and their biogenesis and action is still a significant challenge. It's important to acknowledge that the plant genome has evolved to contain a sophisticated and precise regulatory system through natural selection. A biased explanation of gene expression regulation based solely on structure, function, and mechanism is insufficient. Various components such as functional proteins, transcription factors, ncRNAs, small peptides, and epigenetic modification interact to create intricate networks that finely regulate gene expression in plant development and stress responses. Therefore, future research on sRNAs in plants should prioritize functional analysis and the development of transgenic crops that would be robust and proof of climatic fluctuations and exhibit consistent expression of desired agro-economic traits.

**Acknowledgements** The authors express their gratitude to the Council of Scientific & Industrial Research (CSIR)-University Grant Commission (UGC), New Delhi, India for financial support in the form of Senior Research Fellowship to Miss. Rinku Mondal (2018-MAY-351826) and Mr. Adwaita Das (09/025(0250)/2018-EMR-I)

The authors would like to acknowledge Department of Botany, The University of Burdwan for research and infrastructure facilities.

**Author contributions** RM and AD wrote the manuscript. AB provided the critical comments and edited the manuscript.

## Declarations

**Conflict of interest** The authors have no conflict of interest to disclose.

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