Non-Coding RNAs in Response to Drought Stress

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Abstract: Drought stress causes changes in the morphological, physiological, biochemical and molecular characteristics of plants. The response to drought in different plants may vary from avoidance, tolerance and escape to recovery from stress. This response is genetically programmed and regulated in a very complex yet synchronized manner. The crucial genetic regulations mediated by non-coding RNAs (ncRNAs) have emerged as game-changers in modulating the plant responses to drought and other abiotic stresses. The ncRNAs interact with their targets to form potentially subtle regulatory networks that control multiple genes to determine the overall response of plants. Many long and small drought-responsive ncRNAs have been identified and characterized in different plant varieties. The miRNA-based research is better documented, while lncRNA and transposon-derived RNAs are relatively new, and their cellular role is beginning to be understood. In this review, we have compiled the information on the categorization of non-coding RNAs based on their biogenesis and function. We also discuss the available literature on the role of long and small non-coding RNAs in mitigating drought stress in plants.

Keywords: epigenetic silencing; long non-coding RNA; miRNA; regulatory networks; stress response; water deficit

1. Introduction

About 80–95% fresh biomass of non-woody plants is occupied by water, which plays an important role in many aspects of plant life. Several abiotic factors, such as low rainfall, salinity, very high or very low temperature and high intensity of light lead to water deficit in plants [1]. The reduction in water exerts stress leading to changes in the physiological, morphological, ecological, biochemical and molecular characteristics [2,3]. These changes can affect overall plant development resulting in yield reduction and/or plant loss [4]. In arid and semi-arid environments, drought is one of the most important stress factors for plants [1,4,5]. The continuous increase in environmental temperature has increased the probability of occurrence, duration and severity of drought, thereby making it challenging to meet the global food demands of the ever-increasing world population [6,7].

Drought stress tolerance is a quantitatively controlled trait in plants [8,9]. It causes changes in gene-expression patterns, water transport and osmotic balance, oxidative homeostasis and repair mechanisms. This affects the vital metabolic processes, chlorophyll synthesis and photosynthesis, decelerates seed germination, reduces stomatal movement, inhibits root development and limits nutrient uptake [3,6,10]. As sessile organisms, plants have evolved several mechanisms to withstand water stress and/or drought by inducing changes at the developmental and functional levels [5,9,11,12]. The resistance mechanisms include strategies for avoiding, escaping, tolerating and recovering from drought [13]. To tide over short periods of drought or ‘drought escape’ plants have the ability to regulate growth [10,11]. Once the stress is over, plants resume growth to overcome drought injury and this is known as drought recovery [13].
An important universal physiological process to overcome drought stress involves regulating stomata movement to control respiration, transpiration, photosynthesis and temperature [11,14,15]. Plants can also endure severe water-stress scenarios through osmotic adjustments and accumulation of dehydration-induced proteins [10,12,16,17]. The other changes include regulating the onset of senescence and fine-tuning of phytohormones [2,9,10,12,16] (Figure 1). Plants also modulate the redox pathway by balancing the production of antioxidant enzymes, such as including superoxide dismutase, peroxidase and ascorbate peroxidase, to scavenge the reactive oxygen species (ROS) produced during drought stress [18]. This also helps to maintain organelle stability, protect chloroplast membranes and stabilize the PSII system [19]. Therefore, it is important to identify the factors that regulate the genetic components and govern the nature of plant response.

Figure 1. Schematic representation of different drought stress-response mechanisms operative in plants. The combined actions of these processes govern plant survival or susceptibility. The survival of plants can be grouped under drought avoidance, drought tolerance and drought escape, based on the plant response. ABA = abscisic acid, CSI = chlorophyll stability index, MSI = membrane stability index, PPO = polyphenol oxidase, ROS = reactive oxygen species, RWC = relative water content.

Relatively recent studies have shown that long and small non-coding RNAs (ncRNAs) are important modulators of drought tolerance in plants [12,20–24]. The networking between ncRNAs and their target genes is, in turn, controlled by various other enzymatic components in the cell [9,25]. The advances in high-throughput analysis, such as RNA sequencing (RNA-Seq) and bioinformatics, have accelerated scientific research [26]. Sequence analysis has proved to be an important tool to explore the differences in response to stress between sensitive and tolerant plants, such as sorghum [27], tomato [28], coffee [29], cassava [30], peanut [31], Populus [32], Trifolium [33], wheat [34], rice [35] and maize [36,37]. This has led to the identification of stress-responsive gene expression; however, our knowl-
edge about the regulatory processes is still limited. This review highlights important updates on the available literature on the role of long and small ncRNAs in response to drought stress response in plants.

2. Long Non-Coding RNAs

Over the last decade, long ncRNAs (lncRNAs), usually >200 nucleotides (nt) in size, have emerged as a pivot of genome regulation, adding a new layer of epigenetic control [38–40], but their clear evolutionary origins and functional specialization are still inexplicit. This group of ncRNAs lacks polypeptide-coding potential and possesses significant biochemical versatility, with each lncRNA having specific functions [39,41,42]. High-throughput RNA-Seq based investigations have primarily contributed to the identification of lncRNAs in many organisms [43]. Many investigations have been performed in humans and animals [44–46]; however, in plants, only a few molecules have been well characterized [39,47,48].

In eukaryotes, transcription followed by processing of the nascent RNA precedes the formation of messenger (mRNA). The biogenesis of a fully mature mRNA requires the coordinated action of enzymes that perform 7-methyl Guanosine (m7G) capping, splicing, polyadenylation, maturation, export and surveillance [49,50]. In a similar manner, primary transcripts of lncRNAs, which are produced by RNA Polymerases II or III and IV or V, undergo polyadenylation, m7G capping and splicing [24,51]. Most plant lncRNAs are polyadenylated, but in mammals and yeast, some non-polyadenylated lncRNAs have been found [52]; therefore, the presence of non-polyadenylated functional lncRNAs in plants cannot be completely ruled out [53]. The non-polyadenylated lncRNAs are processed by Ribonuclease P to generate free ends that are stabilized by the capping of small nucleolar RNA (snoRNA). In some cases, the snoRNAs have been found at both 3′ and 5′ ends. Reports have also shown that Ribonuclease P processed free ends can self-ligate to form circular structures [39,40,54,55].

Based on their biogenesis and location, the lncRNAs can be classified into several subgroups [56], as described below.

(a) Long intergenic ncRNAs (lincRNAs) are 200 to 2000 nt in length. These transcripts are derived from the intergenic region and have also been referred to as large/long intervening ncRNAs, very long intervening ncRNAs and macroRNAs [24,57]. They are polyadenylated, weakly spliced, exhibit tissue-specific expression and possess a trans-regulatory role [39,58]. These lncRNAs are characterized by rapid turnover rates, which present a challenge in understanding their functional significance [39,59]. The lincRNAs are localized at least 5 kb away from protein-coding regions and are, therefore, said to lie in gene deserts [60]. These have been sub-classified based on their association with specific regions [61,62], such as enhancer RNAs or eRNAs [52,60], upstream antisense RNA (uaRNA), promoter-associated long RNA (PALR) or promoter upstream transcripts (PROMPTs) [63] and telomeric repeat-containing RNA (TERRA). The PROMPTs and eRNAs are short-lived lncRNAs that have been identified mostly in humans.

(b) Transposable element (TE)-derived lncRNAs (TE-lncRNAs) are generated from the TEs [57]. These transcripts can sometimes act as precursors to microRNAs (miRNAs) and small interfering RNAs (siRNAs) [64–66]. In Arabidopsis, rice, maize and tomato TE-lncRNAs were reported, and their association with response to abiotic stresses was revealed [67–70]. TEs, also known as jumping genes, were first discovered in maize in the early 1950s [71]. They have the ability to copy/cut and paste themselves into other genome regions [72]. Based on the mechanism of transposition, they have been classified as Class I or RNA mediated/retro-elements and Class II or DNA elements. Class II classical TEs transpose via a cut-and-paste mechanism, while Class I TEs transpose through a reverse-transcription-based copy-and-paste mechanism. The DNA copy thus generated can get integrated anywhere in the plant genome [65,72,73]. In the maize genome, more than 85% of DNA is derived from TEs [72,74], so, correspondingly, a large number of TE-lncRNAs have been predicted to be present in maize [75,76].
(c) Intron-derived lncRNAs (incRNAs) originate from within the introns of protein-coding genes [77] and include totally intronic RNA (TIN) or partially intronic RNA (PIN). These transcripts therefore, are regulated by various transcription activation pathways [78]. The incRNAs may contain poly(A) modifications and are usually stable but they may not be highly conserved across different plant species [44,79]. It was reported that few miRNAs and snoRNAs originate from the intronic regions, so, initially, it was considered that the incRNAs may act as progenitors of the small ncRNAs; however, recent studies have confirmed their independent existence [80–82].

(d) Natural antisense transcripts (NATs) originate from coding regions (both exon and intron) in eukaryotic genomes and are amongst the widespread lncRNAs. They possess both cis and trans-action to regulate gene expression by silencing [83,84]. Cis-NATs are transcribed from the inverse strand of the target genomic locus to regulate the corresponding sense transcript [83]. Trans-NATs arise from a locus away from that of the target gene [83,85]. The binding of NATs triggers the production of specific siRNAs, which also exhibit a predominantly trans mode of action.

(e) Circular lncRNAs (circncRNAs) are highly conserved but low in abundance and are more stable than linear lncRNAs, as they cannot be degraded easily [86]. They were first characterized as non-polyadenylated circular RNAs in plant viroids [87]. CircncRNAs mostly arise in the nucleus from the back-splicing of exons in pre-mRNAs [39,86,88,89], while some arise in the cytoplasm. It is postulated that the failure of intronic lariat debranching during canonical splicing plays a role in the biogenesis of circncRNAs [88,90–92]. Most circncRNAs may consist of one or more extra exons and are categorized as extra-exon circular ncRNAs (eicircncRNAs), and others may be derived from the intron region of the parent gene and called circular intronic RNAs (circincRNAs) or intron retained circular ncRNAs; however, some arise from overlapping regions and are called exon-intron circincRNAs (eicircncRNAs) [90,93]. Since circncRNAs are derived from the internal exon regions, they can affect the splicing of their linear counterparts. They have been shown to regulate cell development by acting as endogenous target mimics (eTM) of miRNAs, miRNA sponges [43,91], protein scaffolds or templates for protein translation. The circncRNAs present in exosomes were shown to regulate the proliferation of the respective cells [92].

2.1. Function of IncRNAs

It is clear that a large number of IncRNAs are transcribed in plant cells, but their molecular mechanism is largely unknown [94–98]. They mainly play a regulatory role by facilitating gene silencing to control transcriptional regulation and genome imprinting. These regulations are associated with diverse biological processes, such as root organogenesis [99], photo-morphogenesis [100], control of flowering time, reproduction, nutrient homeostasis [95] and so on [58,67,101]. Their expression levels vary significantly in different tissues and over different developmental stages. The IncRNAs also undergo dynamic regulatory adjustments during the response to abiotic stress [96,102–106] and pathogen invasion [101].

It has been generalized that the Pol IV transcribed IncRNAs serve as precursors for siRNAs, while Pol V transcribed IncRNAs act by modulating the chromatin framework [107]. The IncRNAs can act in cis or trans orientation, forming simple and complex networks. For instance, in Arabidopsis, ~1400 light-responsive NATs were identified, and they could act in both the same and opposite directions [106,108]. They may act as signal molecules guide molecules, precursors for miRNAs and siRNAs, regulators of pre-mRNA splicing and modulators of chromatin [70,107,109–111]. Some of the identified functions of IncRNAs are listed in Table 1.
Table 1. Functions of lncRNAs identified in various plants.

| Plant                | IncRNA Name                         | Pathway                        | Functional Annotation                                                                 | References  |
|----------------------|-------------------------------------|--------------------------------|--------------------------------------------------------------------------------------|-------------|
| Arabidopsis          | IPS1 IncRNA                          | Phosphate homeostasis          | Target mimic for miR399, which regulates PHO2, a negative regulator of the phosphate transporters | [112]       |
|                      | *Hidden Treasure 1* (*HID1*)          | Photomorphogenesis             | Promotes photomorphogenesis in continuous red light by directly repressing *Phytochrome Interacting Factor 3* (*PIF3)* | [100]       |
|                      | ASCO-IncRNA and NSR                   | Alternate splicing module      | Recognizes alternatively spliced mRNA targets                                         | [111]       |
|                      | Drought Induced lncRNAs (DRIR)        | Drought response               | Positively regulates several drought responsive transcripts such as ABA-signal transducers (*P5CS1, RD29A,B and AB15*); annexins (*ANNA17*) and aquaporins (*TIP4, NIP1*) | [113]       |
| Brassica napus, (Q2 and Qinyou8) | XLOC_042431 and XLOC_071559          | Hormone signaling              | Targets *BnaC06g05090D* gene to regulate ethylene metabolism, IAA, Cytokinins and ABA signaling | [114]       |
|                      | XLOC_095305 and XLOC_100682          |                                | Targets *BnaA01g17750D* genes to regulate alpha trehalose phosphate synthase           |             |
|                      | linRNA340                            | Target mimicry                 | miR169 target mimicry, also targets *Nuclear Factor Y* (*NF-Y*)                        |             |
|                      | TCONS_00003360, TCONS_00015102,      | Signal transduction            | Calcium and ABA signaling                                                             |             |
|                      | TCONS_00149293                        |                                | Ethylene metabolism                                                                   |             |
|                      | TCONS_00097416                        | Hormone signaling and target mimicry | Targets *CSLD5, ERL1* and *SPCH* genes to modulate ethylene signaling; |             |
|                      | TCONS_00069665                        |                                | Targets *LAX2, HDG11* and *SCR* genes; and regulates expression by targeting miR156  |             |
|                      | TCONS_00068063, TCONS_00068353       |                                | Targets *CYP707A1* gene and regulates in ABA catabolism                              |             |
|                      | TCONS_00040721                        | MiRNA target                   | Targets *GRF1, HB51* and *DOX1*; regulates gene expression by targeting miR156, miR164, miR169 and miR172 |             |
| Cassava (TMS60444 and Ku50) | MSTRG.25585.13                      | Metabolic pathway              | Regulates sucrose metabolism                                                          |             |
|                      | MSTRG.42613.1                         |                                | Regulates starch metabolism                                                            |             |
|                      | MSTRG.43964.1, MSTRG.4400.2          | Hormone signaling and target mimicry | Targets ABA pathway and related genes, regulates miR164, miR166, miR393 and miR397a,b and act as endogenous target mimic | [97]       |
| Cleistogenes songorica | XLOC_033252                          | Hormone signaling              | Regulates ABA synthesis and signaling by targeting *Pwwr.0184* gene                   | [117]       |
| Panicum virgatum (Alamo) | linRNA20, linRNA2752, linRNA2962, linRNA1039, linRNA3241 | miRNA regulation              | Control drought stress by regulating ptc-miR476 and ptc-miR169                        |             |
### Table 1. Cont.

| Plant                  | IncRNA Name          | Pathway                                      | Functional Annotation                                                                 | References |
|------------------------|----------------------|----------------------------------------------|---------------------------------------------------------------------------------------|------------|
| *Oryza sativa*         | IncRNA MSTRG69391    | Transcription regulation                     | Regulates biological process by targeting genes encoding calmodulin                   | [96]       |
|                        | IncRNA MSTRG41712    | Translation inhibition                        | Targeting genes encoding heat shock protein and mitochondrial carrier proteins          |            |
|                        | and MSTRG68635       |                                              |                                                                                       |            |
|                        | IncRNA MSTRG65848,  |                                              | Upregulated and downregulated the IncRNAs themselves; response to drought stress and     |            |
|                        | MSTRG27834 and       |                                              | targets several genes                                                                  |            |
|                        | MSTRG46301           |                                              |                                                                                       |            |
| *Oryza sativa* cv      | NATOs02g0250700–01   | Differential regulation                       | Regulate response to drought by targeting Os02g0250600-01 (encodes highly abundant     | [119]      |
|                        | andOs02g0180800–01   |                                              | protein during late embryogenesis) and Os02g0180700-01 (encodes Cinnamoyl-CoA reductase) |            |
| *Triticum aestivum*    | c70772_g2_i1 and     | IncRNA-miRNA-mRNA network                    | Targets c69036_g1_i1 and c9653_g1_i2 genes to regulate drought stress                   | [120]      |
|                        | c90557_g1_i1         |                                              |                                                                                       |            |
| *Zea mays*             | Li_TCONS_00080887,   | miRNA targets or decoys                      | Targets or decoys of zma-miR156e-3p, zma-miR156h-3p, zma-miR159c,d-3p, zma-miR159e-5p,| [59]       |
|                        | Zhang_TCONS_00012690,|                                              | zma-miR160b,g-3p, zma-miR160c-3p, zma-miR162-5p, zma-miR164b-3p, zma-miR164d-3p,       |            |
|                        | 625-646,             |                                              | zma-miR164e-3p, zma-miR166h-5p, zma-miR166i-5p, zma-miR166n-5p, zma-miR169c-3p, zma-     |            |
|                        | Boerner_Z27kG1_14953,|                                              | miR169f-3p, zma-miR169l-3p, zma-miR169m-3p, respectively, etc.                          |            |
|                        | Boerner_Z27kG1_09751,|                                              |                                                                                       |            |
|                        | Boerner_Z27kG1_15115,|                                              |                                                                                       |            |
|                        | Boerner_Z27kG1_08283,|                                              |                                                                                       |            |
|                        | Boerner_Z27kG1_16361,|                                              |                                                                                       |            |
|                        | Boerner_Z27kG1_23317,|                                              |                                                                                       |            |
|                        | Boerner_Z27kG1_13892,|                                              |                                                                                       |            |
|                        | Boerner_Z27kG1_01046,|                                              |                                                                                       |            |
|                        | Boerner_Z27kG1_22106,|                                              |                                                                                       |            |
|                        | Boerner_Z27kG1_03819,|                                              |                                                                                       |            |
|                        | Boerner_Z27kG1_17085,|                                              |                                                                                       |            |
|                        | Boerner_Z27kG1_06707,|                                              |                                                                                       |            |
|                        | Boerner_Z27kG1_17308,|                                              |                                                                                       |            |
|                        | Boerner_Z27kG1_01291,|                                              |                                                                                       |            |
|                        | Boerner_Z27kG1_22188,|                                              |                                                                                       |            |
|                        | Boerner_Z27kG1_15675,|                                              |                                                                                       |            |
|                        | Boerner_Z27kG1_06005,|                                              |                                                                                       |            |
|                        | Zhang_TCONS_00011169,|                                              |                                                                                       |            |
|                        | etc.                 |                                              |                                                                                       |            |

2.1.1. IncRNAs as Target Mimics

The IncRNAs can regulate transcription directly or by acting as target mimics of the small ncRNAs [57,124,125]. Some IncRNAs, such as IPS1 (*induced by phosphate starvation*) and ASCO (*alternative splicing competitor*), contain sequences complementary to that of the miRNAs, so they can act as decoys or sponges or eTMs by competing for miRNA binding [59,112,125,126]. The mimic sites within the IncRNAs are non-cleaveable and block
the miRNA function, thus conferring translational regulation in cis orientation. Several of these target mimics are thought to have a role in plant growth and development [127].

The discovery of the IPS1 gene in Arabidopsis introduced the concept of eTMs and unveiled the novel cellular mechanism behind the regulation of the miRNAs [128]. IPS1 contains a region complementary to miR399, but it has a loop at the cleavage point of miR399. Thus, IPS1:miR399 forms a stable pair and quenches the silencing activity of the miRNA. Both IPS1 and miR399 expression are induced upon phosphate starvation and IPS1 expression seems to be required for fine-tuning of miR399 activity [112]. Subsequently, it was shown that IncRNA23468 functions as a decoy for miR482b to compete with transcripts of NBS-LRR genes [129].

The ASCO-lncRNA binds to transcripts encoding nuclear alternative splicing regulators, AtNSRa and AtNSRb to regulate lateral root development [111]. In addition, IncRNA16397 targets sGRX22 (glutaredoxin gene) to induce the expression of GRX21 and reduce ROS accumulation [130]. The dual regulators act to modulate gene expression during Phytophthora infestans infection in tomatoes.

Reports have also indicated that lncRNAs can be targeted and cleaved by the miRNAs [118,131,132]. A computational study by Fan et al. [59] found 466 maize lncRNAs as targets of 165 miRNAs and 86 lncRNAs as decoys for 58 miRNAs. In Populus, about 51 lncRNAs were reported as putative miRNA targets and 20 lncRNAs were reported as target mimics of the known miRNAs in response to drought stress [118]. In Cleistogenes, RNA-Seq analysis identified 52 lncRNAs as target mimics for miRNAs [97]. These analyses clearly showed that lncRNAs are associated with the miRNA nodes and supported their regulatory role in plants.

2.1.2. lncRNAs in DNA Modification

Numerous reports have indicated that, in plants, the lncRNAs participate in the modification of DNA at different developmental stages [105] such as reproduction [133], embryogenesis [134] and organogenesis [92] under stress conditions. The classical example is provided by cold-induced incRNA, COOLAIR, which inhibits FLC (Flowering Locus C) during vernalization to regulate the flowering time in Arabidopsis [135]. The repression is achieved by enrichment of Polycomb repressive complex 2 (PRC2) and subsequent trimethylation of Histone H3 Lysine 27 (H3K27me3) at the FLC locus [136].

Epigenetic silencing via DNA methylation and histone modification is an important mechanism for regulating gene expression. It is specifically significant for controlling transposons, repetitive sequences and centromeric regions and for imprinting [48,70,137]. The lncRNAs can also guide gene silencing through siRNA-dependent DNA methylation [47]. The role of small RNA-directed DNA methylation (RdDM) and heterochromatinization has been well studied in plants [138–140]. The plant-specific RNA polymerases, RNA Pol IV and V play a crucial role in this process [24,51,141–144]. Briefly, Pol IV, along with the CLASSY chromatin remodeling factors (CCRFs) and homeodomain transcription factors, such as DTF1/SHH1, transcribes transposons and repetitive sequences. The transcripts are converted to double-stranded RNAs (dsRNAs) by the action of RNA-dependent RNA polymerase-2 (RDR2) and the dsRNAs are processed into small ncRNAs, specifically siRNA duplexes by Dicer-like 3 (DCL3) enzyme [138,139]. These siRNAs are loaded in Argonaute 4 (AGO4)-containing complex to guide RdDM. In an alternate pathway, siRNAs are generated through Pol I–RDR6 transcription and are loaded into the AGO6 complex. At loci where Pol V is producing nascent transcripts, the siRNA-guided AGO4,6 complex interacts with the larger subunit of RNA Pol V, NRPE1 [145,146]. This complex is stabilized by the KTF1 (yeast transcription elongation factor, SPT5 homolog) to subsequently establish DNA methylation through domains rearranged methyltransferase 2 (DRM2) [141,146]. The methylated state of DNA is maintained through cell divisions through pathways catalyzed by methyltransferase1 (MET1) or chromomethylase3 (CMT3) [117,147].

It was shown that RdDM regulates the repetitive intergenic elements and their expression in maize. The RdDM function is supported by mediator of paramutation 1 (MOP1-1)
in maize, which is an ortholog of At-RDR2 [148]. It was shown that MOP1 copies the RNA Pol IV transcript for processing into siRNAs [144]. In another study, 110 maize lincRNAs and 46 genic lncRNAs were predicted as precursors for Mop1-sensitive siRNAs [149]. In addition, 26 lincRNAs and 97 genic lncRNAs were predicted as precursors for shRNA, while one lincRNA and two genic lncRNAs were predicted as precursors for miRNA. RdDM is a complex pathway that has also been implicated with short-term and long-term stress memory [105], so further investigations are required to understand the role of lincRNAs in regulating RdDM functions in maize in response to drought and other abiotic stresses.

3. Small Non-Coding RNAs

The small ncRNAs comprise a number of categories among which the miRNAs and siRNAs constitute the major groups. They function as key regulators of transcriptional and post-transcriptional gene expression [139,150–152] and are therefore implicated in the control of various physiological and developmental processes in plants, such as growth, organ formation, phase transition, nutrient balance and stress response [10,22,153–156]. Several online tools and databases have been developed that have enabled the prediction, documentation and analysis of the small ncRNAs and their targets [48,57,124]. Deep sequencing and degradome analyses, coupled with advanced tools and databases, have driven the identification of various small ncRNAs in response to single or combined abiotic stresses [20,157–159].

3.1. Small Interfering RNAs

Overall, siRNAs are generally 21–24 nt in length and are produced by the sequential processing of long dsRNAs in a phased or non-overlapping manner. They may arise either from endogenous sources, such as TEs, repetitive elements and centromere, or exogenous sources, such as invading viruses or aberrant inverted repeats [139,160]. The siRNAs can target endogenous as well as exogenous sequences serving as the first line of host defense [161]. The long dsRNAs are processed by DCLs into mature siRNAs, which get associated with AGO protein to form the catalytic core of the RNA-induced silencing complex (RISC) to facilitate gene silencing [139,162]. The siRNA strand that directs the RISC complex is called the guide strand, while the other strand is known as the passenger strand. The passenger strand is excluded and undergoes degradation, while the guide strand directs RISC to its target transcript for cleavage. The identity of the guide and passenger strand is regulated on the basis of the thermodynamic stability of 5′ end [163,164]. The siRNAs also mediate transcriptional gene silencing through the RNA induced transcriptional silencing (RITS) complex [139].

The siRNAs are involved in regulating gene expression, maintaining genome stability and aiding plant defense. In Arabidopsis, DCL2 and DCL4 are involved in production of primary siRNAs from aberrant dsRNAs. DCL2 processes 22 nt siRNAs that contribute to the antiviral defense and plant development while DCL4 processes 21 nt siRNAs to initiate primary defense against invasion of viruses and transgenes [113,139]. The DCL3 processes 24 nt siRNAs to direct methylation of DNA sequences resulting in chromatin modification and transcriptional gene silencing [142,145]. The functions of DCL2 and DCL4 are partially redundant and they are also involved in biogenesis of secondary or transitive siRNAs. The secondary siRNAs are processed from dsRNA produced by the action of RDR6 and SGS3 on single stranded RNA templates that are primed by primary siRNAs [139].

Depending on their site of origin, the siRNAs are classified as repeat-associated siRNA (rasiRNA), trans-acting siRNA (tasiRNA), natural-antisense siRNA (nat-siRNA), heterochromatic siRNA (hc-siRNA) and vi-siRNA (viral siRNAs).

(a) Ra-siRNAs are derived from TEs and repetitive DNAs [165] and mainly function in the silencing of retrotransposons and various abiotic stress factors, including drought [166]. Studies in maize and Arabidopsis have indicated complex feedback regulatory loops between rasiRNA and their target RNAs [166,167].
(b) TasiRNAs are derived by phased cleavage of dsRNA, which is produced after miRNA-mediated cleavage of the TAS gene-derived transcripts. In Arabidopsis, TAS1 and TAS2 transcripts are targeted by miR173, TAS3 transcripts are recognized by miR390 and TAS4 is targeted by miR828 [168]. They play a crucial regulatory role in development through post-transcriptional silencing [169,170]. TAS1, TAS2 and TAS3 were downregulated in response to drought and salinity stress [171]. The tasiRNA-ARF (auxin response factor) module is involved in regulating flower morphogenesis under drought and salt stress [172].

In Sorghum bicolor, two TAS3 gene homologs were identified to regulate the response to drought stress [170].

(c) Nat-siRNAs are a class of functional siRNAs, which originate from within the annealed regions of the natural antisense transcript (NAT) pairs [173]. Scientific evidence has indicated that NATs and Nat-siRNAs are involved in regulating various biological processes of plants and animals, such as phosphate homeostasis [174], stress response [175,176], chromatin remodeling and RNA editing [176–179].

(d) Hc-siRNAs are derived from heterochromatic intergenic regions including repeats and transposons [180]. The hc-siRNAs recognize the nascent Pol V-dependent transcript via base-pair complementarity and guide the DNA methylation and histone modification machinery to the loci for transcriptional gene silencing [180–182]. Their role has been reported in plants in response to several biotic [183–186] and abiotic stress factors [187,188].

(e) Vi-siRNAs are derived from dsRNA replicative intermediates of viruses to induce specific antiviral immunity [189]. They are generally processed from the sense strand of the viral genome [190]. Most of the vi-siRNAs have 5′ monophosphate, which indicates that vi-siRNAs can be produced by the viral RDR [191]. The role of vi-siRNAs has been reported in response to viral pathogen response in different plants, such as Arabidopsis [192], tomato [193], soybean [194], tobacco [195] and so on.

3.2. MicroRNAs

The miRNAs are processed from long primary transcripts that are transcribed from the genome. The steps in their biogenesis are complex and intricately regulated, as it involves the coordination of several proteins [196]. The primary transcripts (pri-miRNA) are sequentially processed by the DCL1 containing microprocessor complex into precursor miRNAs (pre-miRNA) and then into mature miRNAs. The steps in miRNA biogenesis are illustrated in Figure 2. Several other proteins, such as HYL and SE, are required for accurate DCL1 function [197]. The mature miRNA duplex is then methylated at the ends by HEN1 and transported to the cytoplasm, where it gets associated with the AGO containing RISC to form a functional complex, which can bring about transcript cleavage or suppress translation [198–200].

The miRNAs regulate various aspects of plant growth and development (Table 2) by regulating tissue or organ differentiation and development, shoot branching, root branching, lateral root development, panicle formation, flower development, seed development, primordial development, apical dominance, etc. [150,156,199–206]. The miRNAs also play an important role in promoting adaptation and tolerance to fluctuations in environmental conditions [207–210]. Moreover, miRNAs act in a coordinated manner by controlling the network of key genes, transcription factors and phytohormones [208,211–214].
Figure 2. Generalized scheme to illustrate the various steps involved in plant miRNA biogenesis and activity. The miRNA genes are transcribed to primary miRNA transcripts (pri-miRNAs) of 100–120 nt long by RNA polymerase II that are then capped and polyadenylated. In the first maturation step of miRNA synthesis, pri-miRNA is cleaved by DCL1 in collaborative action of other enzymes to form precursor miRNA (pre-miRNA) of approximately 70–100 nt long. In the second maturation step, the hairpin structured pre-miRNA is processed by the same enzymes to mature miRNA duplex. The DCL1 cleavage results in the formation of a miRNA–miRNA* duplex of 21 to 24 nt containing two nucleotide 3′ overhangs and 5′ monophosphate regions. This duplex is transported out of the nucleus and into the cytoplasm, where it associates with an AGO (Argonaute) containing protein complex to form RNA induced silencing complex (RISC). The RISC is guided to the target sequence of single-stranded mRNA. Depending upon the nature of miRNA and AGO, the target mRNA is either cleaved or subjected to suppression of translation.

It was seen that mutants in the miRNA biogenesis pathway exhibited an impaired response to abscisic acid (ABA), auxin and cytokinins [213,215], thus indicating the overlapping of regulatory hubs in plants. Later, it was shown that miR159 and miR164 modulated the levels of gibberellic acid (GA) and auxin, respectively [216–218]. The transcripts for auxin receptors, TIR1 (transport inhibitor response-1) and F-box protein 2 are targeted by miR393 [219–222]. The miRNA expression levels are also modulated by hormones, as exemplified by the downregulation of miR167 after treatment with ARF [223].

The first direct evidence that miRNAs are involved in plant stress responses came from the work of Jones-Rhoades and Bartel in the year 2004. Abiotic stress-regulated miRNAs were first reported in the model plant Arabidopsis thaliana [224] and, by now, the stress-responsive miRNAs have been reported in almost all plant species [225–229]. Functional
studies have also supported this role for miRNAs. For example, overexpression of miR393 reduced plant growth in drought stress by downregulating the auxin signals [230]. There are also reports on the functional involvement of the miRNA passenger strand (miRNA*) in various responses. For example, miR169g* and miR172b* were downregulated in tomato leaves under varying phosphate deficient conditions [199,231].

Plant miRNA activity is precisely controlled by the regulation of expression of miRNA genes, processing of mature miRNAs and function of miRNAs. The first level of control involves the development and tissue-specific regulation of pri-miRNA transcription in response to hormonal and environmental cues by a variety of transcription factors [232,233], such as ARF, LFY, MYC2, etc. The transcripts of many of these transcription factors are regulated by the miRNAs, indicating the existence of complex cellular feedback loops [234].

The second level of control is achieved by regulating the processing or biogenesis of mature miRNAs. This is indicated by differences in the levels of pri/pre-miRNA and mature miRNAs and by the presence of DCL3 dependent 24 nt long miRNAs [169,235]. The regulation of DCL1 transcripts by miR162 and AGO1 transcripts by miR168 also adds to the spatial or temporal differences in miRNA activities [236]. In 2008, it was reported that overexpression of SINEs (short interspaced elements) resulted in phenotypes similar to that of miRNA-deficient mutants. Later, it was discovered that stem-loops of SINEs mimic the pre-miRNAs to bind and quench HYL1 [237].

The third level of control can be achieved by sorting miRNAs in different AGO complexes. According to the most popular hypothesis, the 5′-terminal nucleotide of miRNA guide strand determines the selection of the specific AGO containing RISC and, hence, the subsequent mode of action [238,239]. For instance, Urudine at the 5′ end supports preferential sorting with AGO1, whereas adenosine at the 5′ end favors sorting with AGO2 and AGO4 [240].

Table 2. List of conserved miRNAs and their key target genes that function in plant growth and development.

| miRNAs       | Target Gene       | Functions                                           | References |
|--------------|-------------------|-----------------------------------------------------|------------|
| miR156/157   | SPL               | Phase transition from vegetative to reproductive phase; flowering | [203]      |
| miR159       | MYB family        | Development of male reproductive organs             | [216]      |
| miR160       | ARF10, ARF16      | Controls root development and gravitropism          | [213]      |
| miR165/166   | HD-ZIPIII         | Leaf development and polarity; lamina expansion     | [202]      |
| miR166       | RDD1              | Grain size and weight                               | [204]      |
| miR167       | ARF10, ARF16, ARF17 | Floral patterning; controls anther and ovule development | [241]      |
|              | ARF6, ARF8        | Stamen and gynoecium and maturation; seed development | [214]      |
| miR168       | AGOs              | Leaf polarity                                       | [200]      |
| miR169       | NF-YA             | Floral organ identity                               | [242]      |
| miR172       | AP2               | Floral patterning and floral organ development; regulates the inner whorl organ differentiation | [243]      |
| miR319       | TCP               | Leaf morphogenesis                                  | [226]      |
| miR390       | ARF2, ARF3, ARF4  | Leaf development, adaxial identity of leaf blade, lateral organ development and leaf senescence | [172]      |
| miR394       | Leaf Curling Responsiveness (LCR) | Regulation of leaf curling, shoot meristem differentiation and maintenance in abscisic acid–dependent manner | [244]      |
| miR396       | Growth Regulating Factors (GRFs) | Adaxial–abaxial polarity of leaf and cell proliferation | [245]      |
| miR399       | PHO2              | Control of flowering time                            | [227]      |
| miR408       | Plantacyanin      | Root development                                     | [246]      |
| miR444       | MADS box          | Floral patterning and development control            | [247]      |
4. Role of Long and Small Non-Coding RNAs during Drought Stress

The regulatory functions of plant lncRNAs and miRNAs in plant stress response have been comprehensively studied [67,106,109,251,252]. These two classes of ncRNAs also participate in response to water deficit and drought through complex cellular pathways involving chromatin modulation, target mimicry, transcriptional regulation, hormonal signaling and by directly regulating drought-responsive genes [57,117,158,230,253,254].

4.1. lncRNAs in Drought Stress

Genome-wide transcriptome studies have identified several drought-responsive lncRNAs in different plant species [96,97,115,255–258]. For example, studies on the identification of drought-responsive lncRNAs in grass families detected 664 potential candidates in maize [102], 98 in rice [119], 19 in foxtail millet [259] and 1597 in switchgrass [117]. The various reports on the identification of drought-responsive lncRNAs are presented in Table 3. Most lncRNAs regulate the drought response by acting on genes participating in ethylene and ABA synthesis or signaling, calcium signaling, starch and sucrose synthesis and several other metabolic processes.

### Table 3. Some drought-responsive lncRNAs reported in different plants.

| Plant      | Number of Putative lncRNAs Identified | Platform of Identification | Functional Annotation                                      | References |
|------------|---------------------------------------|----------------------------|-----------------------------------------------------------|------------|
| Arabidopsis thaliana | 303 | qRT-PCR | Responsive to heat, cold, drought and salt stress | [94] |
|            | 13,230 | Transcriptome Analysis, published tiling array datasets | Response to drought, cold, high-salt and/or ABA treatments | [98] |
| Banana     | 8471 | Transcriptome Analysis, HiSeq | Drought stress-response | [260] |
| Cassava    | 682 | HiSeq 2500, qRT-PCR, CNCI, CPC | Hormone signal transduction, sucrose metabolism pathway, etc. | [115] |
|            | 124 | qRT-PCR | Melatonin responsive, drought stress regulation, cellular metabolism, Calvin cycle, hormone regulation, etc. | [116] |
| Chickpea   | 56,840 | RNA-Seq Transcriptome Analysis | Differential expression in cold or drought conditions | [262] |
|            | 3457 | RT-qPCR, PLncPRO | Differentially expressed under drought stress | [257] |
### Table 3. Cont.

| Plant                               | Number of Putative lncRNAs Identified | Platform of Identification | Functional Annotation                                      | References |
|-------------------------------------|--------------------------------------|---------------------------|------------------------------------------------------------|------------|
| *Cleistogenes songorica*            | 3397                                 | HiSeq2500, CPC, CNCI, CPATqRT-PCR | Regulate drought stress response                           | [97]       |
| *Dimocarpus longan* Lour             | 7643                                 | Real-time qPCR            | Early somatic embryogenesis                                | [134]      |
| *Oryza sativa*                      | 98                                   | HiSeq 2500, qRT-PCR       | Regulatory role in drought response                        | [119]      |
| *Panicum virgatum* L                | 3714                                 | RT-qPCR, PLncPRO          | Differentially expressed under drought stress              | [242]      |
| *Populus trichocarpa*               | 504                                  | HiSeq™ 2000, RT-qPCR      | Drought-stress response, putative targets and target mimics of miRNAs | [118]      |
| *Pyrus betulifolia*                 | 251                                  | HiSeq 4000, CNCI, CPC, qRT-PCR | Regulate various metabolic processes                      | [263]      |
| *Setaria italica*                   | 19                                   | HiSeq 2000, qRT-PCR       | Control drought stress response                            | [259]      |
| *Solanum lycopersicum*              | 521                                  | RT-qPCR                   | Variety of biological processes via lncRNA-mRNA co-expression | [264]      |
| *Triticum aestivum* (Kiziltan, TR39477 and TTD-22 varieties) | 59,110, 57,944 and 40,858 | HiSeq 2000, qRT-PCR | Differential expression under drought stress response in cultivated and wild varieties | [120]      |
| *Zea mays*                          | 1724                                 | RT-qPCR                   | Regulatory role in drought response                        | [102]      |
|                                    | 637                                  | Ribosomal RNA depletion and ultra-deep total RNA sequencing | Regulatory roles in response to N stress                   | [265]      |
|                                    | 1535                                 | HiSeq 2500, qRT-PCR       | Oxidoreductase activity, water binding and electron carrier activity | [122]      |
|                                    | 1199                                 | RiboMinus RNA-Seq         | Control drought and salt stress                            | [266]      |
|                                    | 1769                                 | Strand-specific RNA sequencing, | NATs in drought stress response                           | [267]      |

The studies on cassava identified 51 drought-specific differentially expressed lncRNAs and qRT-PCR validation of selected molecules among them revealed the up-regulation of lincRNA101, lincRNA391 and lincRNA356. Other lncRNAs, such as lincRNA64, lincRNA350, lincRNA182 and lincRNA392, were downregulated under drought stress. The TCONS_00060863 and TCONS_00097416 lncRNAs were shown to regulate ABA and ethylene signaling pathways, respectively, under drought stress [116]. In switchgrass, drought stress upregulated the lncRNAs XLOC_053020, XLOC_014465 and XLOC_033252 to control ABA synthesis, XLOC_074836 to regulate ethylene signaling and XLOC_005809 to control trehalose phosphate synthase [117].

In rice, 98 drought-responsive NAT-lncRNAs were identified by using RNA-Seq analysis. These included two important drought-responsive lncRNAs viz NAT Os02g0250700-01 and NAT Os02g0180800-01, which targets the late embryogenesis abundant protein and cinnamoyl CoA reductase genes, respectively [119]. Studies in maize identified that the lncRNAs expressing at the R1 stage (siling stage) had a critical role in drought stress tolerance [122]. The possible role of lncRNAs as positive regulators of drought stress tolerance in Arabidopsis was identified with the discovery of a novel nucleus localized 755 nt long drought-induced...
lincRNA (DRIR). The DRIR overexpressing *Arabidopsis* lines had higher drought tolerance than wild-type seedlings [113]. This lincRNA was a nuclear-localized and controlled transcription of several drought stress-responsive genes, including ABA signaling genes (*ABI5*, *P5CS1*, *RD29A* and *RD29B*), aquaporin genes (*NIP1* and *TIP4*), annexin gene (*ANNAT7*), fucosyltransferase4 (*FUT4*) gene and transcription factor genes (*NAC3* and *WARKY8*) [113].

4.2. miRNAs in Drought Stress

Several studies have also shown the role of miRNAs in regulating plant response to drought stress (Table 4). A number of miRNAs, such as miR156, miR158, miR159, miR165, miR167, miR168, miR169, miR171, miR319, miR393, miR394 and miR396, were upregulated in response to drought stress in *Arabidopsis* [268]. The upregulation of *Arabidopsis* miR393, miR319 and miR397 in response to dehydration was reported earlier [224]. In drought-stressed rice seedlings, genome-wide analysis was carried out across different developmental stages, from tillering to inflorescence formation, using a microarray platform [269]. This analysis identified 30 miRNA gene families that were differentially regulated. Among these, 16 miRNA families, namely miR156, miR159, miR168, miR170, miR171, miR172, miR319, miR396, miR397, miR408, miR529, miR896, miR1030, miR1035, miR1050, miR1088 and miR1126, were significantly downregulated. Meanwhile, 14 miRNAs, namely miR159, miR169, miR171, miR319, miR395, miR474, miR845, miR851, miR854, miR896, miR901, miR903, miR1026 and miR1125, were significantly upregulated under drought stress. Another report showed that miR164c, miR319b and miR1861d were downregulated, while miR166h, miR172d and miR408 were upregulated under drought stress in rice [270]. In rice, pre-miRNA expression profiling indicated that miR171f was involved in the progression of rice root development and growth and response to drought stress [119]. In a different study, it was shown that miR169g was strongly upregulated and miR393 was transiently induced by drought stress in rice [271]. Inoculation of rice plants with *P. indica* caused upregulation of miR396, and this resulted in the downregulation of growth-regulating factor (GRF), which lowered the rate of transpiration and enabled the plants to tolerate drought [272].

### Table 4. Drought-responsive miRNAs reported in different crop plants.

| Plant Name | miRNAs | Target | Target Description | References |
|------------|--------|--------|--------------------|------------|
| *Arabidopsis* | miR160 | ARF | | [273] |
| | miR165/166 | HD-ZIPIII, CLP-1, RDD1, ABA signaling | | [274–276] |
| | miR167 | IAR3 | | [277] |
| | miR169 | NFY-A, HAP2 | | [278] |
| | miR408 | LAC | | [279] |
| | miR397a | MLOC_54246.3 | LAC-23 | |
| | miR399 | MLOC_52822.6 | Phosphatase 2 | |
| | | MLOC_70587.1 | PHD finger protein | |
| | | LOC_50162.1 | Sucrose synthase 1 | |
| | | MLOC_67419.2 | PBS1, Ser/Thr-protein kinases | |
| | | MLOC_67450.11 | D27, beta-carotene isomerase | |
| | | MLOC_73965.1 | Homocysteine S methyltransferase 3 | [280] |
| *Barley* | Novel-m0406-3p | MLOC_34795.2 | RNA polymerase (25-kDa subunit) | |
| | | MLOC_55820.2 | Pectinesterase | |
| | | MLOC_52822.6 | Phosphatase 2 | |
| | Novel-m0793-3p | MLOC_56261.3 | ABC transporter C family member 2-like | |
| Plant Name | miRNAs | Target | Target Description | References |
|------------|--------|--------|--------------------|------------|
| Novel-m1738-3p | MLOC_3895.3 | Dro1 (coding for early auxin response protein) |
| Novel-m1900-5p | MLOC_16998.3 | Glycine-rich RNA-binding protein 10 |
| Novel-m2311-5p | MLOC_61629.2 | Transcription elongation factor, SPT6 |
| Novel-m2328-3p | MLOC_6972.2 | DNA crosslink repair 1A protein |
| miR159 |  | GA-MYB-like |
| miR160 |  | ARF 16 (Seed germination and post germination stages) |
| miR166 |  | ATHB-15 (axillary meristem initiation, leaf and vascular development) |
| miR167 |  | ABI 5 (Gynoecium and stamen development) |
| miR169 |  | NFY-A (plant development and flowering timing; response to different biotic stresses) [281] |
| miR171 |  | NSP2 (response to abiotic stresses and floral development) |
| miR172 |  | RAP2-7 (flowering time, floral organ identity and cold stress response) |
| miR393 |  | AFB2 (susceptibility to virulent bacteria) |
| miR396 |  | CP29 (leaf and cotyledon development) |
| miR408 |  | Plantacyanin (regulation of DREB and other drought responsive gene) [282] |
| Chickpea |  |  |
| Chickpea |  |  |
| Creeeping bentgrass | miR319 | T159 | MYB protein 306-like [283] |
| Creeeping bentgrass | miR159 | T167 | ARF 8-like |
| Creeeping bentgrass | miR170 | T170 | GRAS transcription factor |
| Creeeping bentgrass | miR172 | T172 | Floral homeotic protein, APETALA 2-like |
| Creeeping bentgrass | miR319 | T319 | Transcription factor, MYB75-like |
| Creeeping bentgrass | b-miR-n-07 | TB7 | ATPase |
| Creeeping bentgrass | b-miR-n10 | TB10 | GRAS transcription factor |
| Creeeping bentgrass | b-miR-n24 | TB24 | DELLA protein GAI1-like [284] |
| Cucumis sativus | miR169 | T169 | NFY-A-1-like |
| Cucumis sativus | miR395 | T395 | ATP sulfurylase 1 |
| Cucumis sativus | miR398 | T398 | Superoxide dismutase |
| Cucumis sativus | csa-miR-n19 | TC19 | Pleiotropic drug resistance protein 2-like |
| Cucumis sativus | miR168 | T168 | Argonaute 1A-like |
| Cucumis sativus | miR396 | T396 | Endoribonuclease dicer homolog 1-like |
| Cucumis sativus | b-miR-n02 | TB2 | Pre-mRNA-processing factor 17-like |
| Cucumis sativus | b-miR-n20 | TB20 | Dicer-like protein 4-like |
| Cucumis sativus | miR30a,b | eugene3.00010640 | Electron carrier activity |
| Plant Name | miRNAs | Target | Target Description | References |
|------------|--------|--------|--------------------|------------|
| miR71*     | eugene3.00010640 | Electron carrier activity |
|            | grail3.000824501 | Electron carrier activity |
|            | eugene3.105640001 | Electron carrier activity |
|            | fgenesh4_pg_C_scaffold_263000013 | Electron carrier activity |
| miR77      | eugene3.00002056 | Electron carrier activity |
|            | estExt_Genewise1_v1.C_LG_XIV3469 | Electron carrier activity |
| miR84*     | fgenesh4_pm.C_LG_XIII000061 | Electron carrier activity |
| miR101a    | gw1.1.9350.1 | Transcription factor |
| miR131     | fgenesh4_pg_C_LG_X001404 | DNA binding |
|            | estExt_Genewise1_v1.C_LG_XV2187 | Electron carrier activity |
|            | fgenesh4_pg_C_scaffold_9189000001 | Electron carrier activity |
|            | fgenesh4_pg_C_LG_J001030 | DNA binding |
| miR58      | estExt_Genewise1_v1.C_LG_XV2187 | SBP-box Transcription factor |
| miR67*     | gw1.VIII.1137.1 | Function unknown |
|            | eugene3.00031501 | Vesicle transport v-SNARE |
| miR93a     | grail3.00100018301 | Function unknown |
|            | estExt_Genewise1_v1.C_LG_JV3721 | NADH-ubiquinone oxidoreductase |
| miR93b     | grail3.00100018301 | Function unknown |
| miR106*    | estExt_fgenesh4_pg_C_17020003 | Cytochrome oxidase biogenesis protein |
|            | estExt_fgenesh4_pm.C_1230037 | Function unknown |
| miR115a    | gw1.57.264.1 | Function unknown |
| miR123a    | estExt_fgenesh4_pg.C_LG_J11182 | Development and cell-death domain |
| miR156c    | | Putative protein phosphatase 2C |
| miR159a,b  | | Serine/threonine protein phosphatase |
| miR159a-d  | | GA-MYB transcription factor |
| miR160a-e  | | S16, 40S ribosomal protein |
| miR160b,i  | | ARR11, response regulator |
| miR166l,m  | | Homeodomain–leucine zipper protein |
| miR167a-i  | | ARF 12 |
| miR167c    | | ARF 17, Putative eIF3e |
| miR167i,g  | | ARF 25 |
| miR167d    | | Phospholipase D |
| miR168a,b  | | Serine/threonine-protein phosphatase |
| miR168b    | | Receptor-like protein kinase |
| miR168a,b  | TC250636 | DEAD-box ATP-dependent RNA helicase |
|           | TC251979 | Putative early responsive to dehydration stress protein, |

[286]
Table 4. Cont.

| Plant Name | miRNAs | Target | Target Description | References |
|------------|--------|--------|--------------------|------------|
| TC274109   |        | GTPase |                    |            |
| TC259098   |        | Heat shock protein 90,| |            |
| TC26999    |        | GA-MYB-binding protein | |            |
| miR396d,e |        | Putative serine/threonine protein kinase | |            |
| TC248005   |        | Pyruvate, orthophosphate dikinase, | |            |
| TC253981   |        | Putative protein serine/threonine kinase, | |            |
| TC270251   |        | Putative selenium binding protein, | |            |
| TC270802   |        | Fructose-bisphosphate aldolase | |            |
| miR408     |        | Leucine-rich repeat family protein | |            |
| miR474b    |        | Putative CBL-interacting protein kinase, | |            |
| TC263244   |        | Proline dehydrogenase family protein, | |            |
| miR474c    |        | Putative transcription factor MYB, | |            |
| CF632829   |        | WRKY transcription factor 31 | |            |
| miR528     |        | Cu/Zn SOD, | |            |
| TC274952   |        | Peroxidase | |            |
| MiR827     |        | N/Pi metabolism | |            |
| miR156a/b,c,d,e,g,h,k,l | | DNA-binding putative protein | |            |
| GRMZM2G040785 |        | Unknown | |            |
| GRMZM2G307588 |        | SPL 6 | |            |
| GRMZM2G414805 |        | SPL 11 | |            |
| GRMZM2G460544 |        | SPL 7 | |            |
| GRMZM2G067624 |        | Homoserine kinase | |            |
| GRMZM2G465165 |        | Serine/threonine protein kinase | |            |
| miR159a,b,f,c | | DNA-binding protein | |            |
| GRMZM2G167088 and | | Unknown | |            |
| GRMZM2G416652 |        | | |            |
| GRMZM2G027100 |        | MYB55 | |            |
| miR159a,b,f and miR319a,c | | GA-MYB | |            |
| miR159a,b,f | | DNA-binding protein | |            |
| GRMZM2G423833, | | | |            |
| GRMZM2G075064 |        | | |            |
| miR166d    |        | MPPN domain | |            |
| GRMZM2G003509 |        | Protein methyltransferase | |            |
| GRMZM2G499154 |        | Metabolic process | |            |
| miR167a,c  |        | Hormone stimulus | |            |
| GRMZM2G078274, | | | |            |
| GRMZM2G475882 |        | | |            |
| miR395b    |        | Secondary active sulfate transmembrane transporter (1) | |            |
| GRMZM2G149952, | | ATP sulfurylase | |            |
| GRMZM2G051270 |        | | |            |
| miR396f    |        | Actin binding protein | |            |
| GRMZM2G178990 |        | | |            |
| Plant Name | miRNAs | Target | Target Description | References |
|------------|--------|--------|--------------------|------------|
| miR1432   | miR1436 | GRMZM2G423139 | Calcium-binding allergen Ole e 8 | |
| miR2097-5p | GRMZM2G151955 | RNA binding protein | |
| mir319a-d-3p | GRMZM2G089361T01, GRMZM2G145112 T02, GRMZM2G106579 T02 | TCP family transcription factor | |
| miR393ac-5p | GRMZM2G135978 Tol, GRMZM5G848945_T02 | Putative uncharacterized protein | |
| miR396cd  | GRMZM2G033612 T02 | Putative uncharacterized protein | |
| miR398ab-3p | GRMZM2G023847 Tol, GRMZM2G097851 Tol | Putative uncharacterized protein | |
| miR444ab  | GRMZM2G492156_T01, GRMZM2G033093_T01 | Putative uncharacterized protein | |
| miR529    | GRMZM2G98594_T06, GRMZM2G099862_T04, GRMZM2G119359_T01, GRMZM5G893117 T01, GRMZM2G105335_T02, GRMZM2G067743_T03 | GRF-transcription factor | |
| miR529    | GRMZM2G023847 Tol, GRMZM2G097851 Tol | Putative uncharacterized protein | |
| miR529    | GRMZM2G352678 T01 | Chemocyanin | |
| miR529    | GRMZM5G866053_T01 | Basic blue protein-like | |
| miR529    | GRMZM2G122302_T01, GRMZM2G082940_T01 | Blue copper protein | |
| miR529    | GRMZM2G98594_T06, GRMZM2G099862_T04, GRMZM2G119359_T01, GRMZM5G893117 T01, GRMZM2G105335_T02, GRMZM2G067743_T03 | AP2/EREBP transcription factor protein | | [287] |
| miR529    | GRMZM2G023847 Tol, GRMZM2G097851 Tol | Putative uncharacterized protein | |
| miR529    | GRMZM2G352678 T01 | Chemocyanin | |
| miR529    | GRMZM5G866053_T01 | Basic blue protein-like | |
| miR529    | GRMZM2G122302_T01, GRMZM2G082940_T01 | Blue copper protein | |
| miR529    | GRMZM2G98594_T06, GRMZM2G099862_T04, GRMZM2G119359_T01, GRMZM5G893117 T01, GRMZM2G105335_T02, GRMZM2G067743_T03 | AP2/EREBP transcription factor protein | | [287] |
| miR529    | GRMZM2G023847 Tol, GRMZM2G097851 Tol | Putative uncharacterized protein | |
| miR529    | GRMZM2G352678 T01 | Chemocyanin | |
| miR529    | GRMZM5G866053_T01 | Basic blue protein-like | |
| miR529    | GRMZM2G122302_T01, GRMZM2G082940_T01 | Blue copper protein | |
| miR399    | PHO2, UBC24 | Control Pi homeostasis | | [288] |
| miR399    | PHO2, UBC24 | Control Pi homeostasis | | [288] |
| miR399    | PHO2, UBC24 | Control Pi homeostasis | | [288] |
| miR156    | SPL | Shoot development and delayed change in vegetative phase | | [289] |
| miR160    | ARF (root development and auxin signals) | ARF (root development and auxin signals) | | [288,289] |
| miR166    | HD-ZIPIII (leaf development and polarity) | HD-ZIPIII (leaf development and polarity) | | [288,289] |
| miR169    | HAP2 | Nitrogen homeostasis and stress response | | [289] |
| miR395    | APS, AST | Control ATP Sulfurylase activity | | [289] |
| miR171    | SCL | Regulate root development | | [289] |
| Plant Name                  | miRNAs | Target | Target Description                                                                 | References |
|----------------------------|---------|--------|-------------------------------------------------------------------------------------|------------|
| miR172                     | AP2     |        | Maintain nitrogen remobilization and floral development                               |            |
| miR167                     | CCAAT-binding factor, ARF |        |                                                                                     |            |
| miR397                     | LAC (regulate copper homeostasis and reduces root growth) |        |                                                                                     |            |
| miR159                     | MYB     |        | Regulate flowering time; leaf shape and size                                           | [288]      |
| miR162                     | DCL1    |        | Negative feedback regulatory function                                                | [258]      |
| miR164                     | NAC1    |        | Control lateral root development                                                     | [258,288]  |
| miR168                     | AGO1    |        | Nutrient homeostasis and feedback regulation                                          | [290]      |
| miR2275                    | gnl|GNOMON|155702013.m | Mitochondrial protein                                                               | [254]      |
| miR393                     | gnl|GNOMON|39086093.m | Protein transport inhibitor response 1-like                                          |            |
| miR398                     | CSD     |        | Copper homeostasis and oxidative stress                                              | [291]      |
| miR156k                    | ↓ in drought and submergence |        |                                                                                     |            |
| miR159ab                   | ↑ in drought, ↓ in submergence |        |                                                                                     |            |
| miR164e                    | ↓ in drought and submergence |        |                                                                                     |            |
| miR166b,d                  | ↓ in drought and submergence |        |                                                                                     |            |
| miR167c,d,e,g              | ↓ in drought and submergence |        |                                                                                     |            |
| miR169c,r                  | ↓ in drought and submergence |        |                                                                                     |            |
| miR319b                    | ↑ in drought, ↓ in submergence |        |                                                                                     | [292]      |
| miR396c,d                  | ↓ in drought and submergence |        |                                                                                     |            |
| miR398a,b                  | ↓ in drought and submergence |        |                                                                                     |            |
| miR398b                    | ↓ in drought and submergence |        |                                                                                     |            |
| miR408                     | ↓ in drought and submergence |        |                                                                                     |            |
| miR408b                    | ↓ in drought and submergence |        |                                                                                     |            |
| miR528ab                   | ↓ in drought and submergence |        |                                                                                     |            |
| miR166c                    | Constitutive expression |        |                                                                                     |            |
| *Medicago sativa*          | miR156  | | SBP-like protein                                                                      | [293]      |
| miR164                     | NAC domain transcription factor (lateral root development) ↓ |        |                                                                                     |            |
| miR169                     | CBF (response to drought, cold and salinity, nodule development) ↓ |        |                                                                                     |            |
| *Medicago truncatula*      | miR171  | | GRAS transcription factors (response to drought, cold and salinity, nodule Morphogenesis and floral development) ↓ | [294]      |
| miR396                     | GRF (response to drought and salt; cell proliferation) ↓ |        |                                                                                     |            |
| miR398                     | Cu/Zn CSD1, CSD2 (response to oxidative stress) ↓ |        |                                                                                     |            |
| miR399                     | PHO2    |        | ubiquitin conjugating enzyme balance of phosphorus, ↑                                |            |
| Plant Name | miRNAs | Target | Target Description | References |
|------------|--------|--------|--------------------|------------|
| Rice       | miR167, miR9774, miR939, miR162, miR319, miR156, miR408, miR166, miR331, miR827 and miR8175 | miR167, miR9774, miR398, miR162, miR319, miR156, miR408, miR166, miR331, miR827 and miR8175 | ↓ expression profiling in response to drought stress | [294] |
|            | miR6300, miR160, miR1861, miR440, miR9773, miR3982, miR171 and miR1876 | miR6300, miR160, miR1861, miR440, miR9773, miR3982, miR171 and miR1876 | ↑ expression profiling in response to drought stress | |
| Rice       | 67 novel drought responsive miRNAs | 66 miRNAs | Response to drought stress | [119] |
|            | Osa-miR159f, Osa-miR1871, Osa-miR9398b, Osa-miR408-3p, Osa-miR2878-5p, Osa-miR528-5p and Osa-miR397a | Osa-miR159f, Osa-miR1871, Osa-miR9398b, Osa-miR408-3p, Osa-miR2878-5p, Osa-miR528-5p and Osa-miR397a | ↑ in the flag-leaves of tolerant cultivar (N22 and Vandana, while ↓ in sensitive cultivar (PB1 and IR64) during drought | [296] |
|            | miR398 | CSD | Regulate copper homeostasis and oxidative stress | [292] |
| Sugarcane  | MiR160, miR399 and miR528 | MiR160, miR399 and miR528 | ↑ in tolerant cultivar (RB867515) | |
|            | miR160, miR394, miR399 and miR1432 | miR160, miR394, miR399 and miR1432 | ↑ in sensitive cultivar (RB855536) | [297] |
|            | miR166, miR169, miR171, MiR172, miR393, miR396, miR399 and miR1432 | miR166, miR169, miR171, MiR172, miR393, miR396, miR399 and miR1432 | ↓ in tolerant cultivar (RB867515) | |
|            | miR166, miR171, miR396 | miR166, miR171, miR396 | ↓ in sensitive cultivar (RB855536) | |
| Sunflower  | miR399a-2 | HannXRQ_chr02g0057111 | Environment adaptation; leaf ↑; root ↑ | |
|            | Novel-mir40 4 | HannXRQ_chr03g0090941 | DNA repair protein XRCC; root ↑ | [251] |
|            | Novel-mir3, Novel-mir42 | HannXRQ_chr04g0098561 | Putative toll/interleukin-1 receptor; root ↑ | |
|            | miR396b | HannXRQ_chr04g0115781 | Serine/threonine protein kinase; leaf ↑ | |
| Plant Name | miRNAs | Target | Target Description | References |
|------------|--------|--------|--------------------|------------|
| miR156a-5p,f,k,q, 157a-5p | HannXRQ_chr05g0138971 | SBP transcription factor; leaf ↑ | |
| Novel-mir3 | HannXRQ_chr05g0149501 | P-loop containing nucleoside triphosphate hydrolase; leaf ↓ | |
| miR396a,b-5p | HannXRQ_chr05g0150421 | Glutamyl tRNA reductase and chlorophyll metabolism; leaf ↓ | |
| miR156h | HannXRQ_chr07g0196531 | Leaf ↓ | |
| miR396f-1 | HannXRQ_chr08g0211484 | Serine/threonine dual specificity protein kinase; root ↑ | |
| miR394a-3p-1 | HannXRQ_chr08g0216701 | Related to Zn ion transport; leaf ↑ | |
| Novel-mir36 | HannXRQ_chr08g0219981 | Putative plant disease resistance response protein; root ↓ | |
| Novel-mir42 | HannXRQ_chr09g0239281 | Putative toll/interleukin-1 receptor homology (TIR) domain; root ↑ | |
| Novel-mir3 | HannXRQ_chr09g0239531 | P-loop containing nucleoside triphosphate hydrolase; root ↑ | |
| Novel-mir55 | HannXRQ_chr09g0252001 | C-terminal LisH motif-containing protein, Leaf ↑; root ↑ | |
| Novel-mir42 | HannXRQ_chr13g0396521 | P-loop containing nucleoside triphosphate hydrolase; root ↑ | |
| Novel-mir3 | HannXRQ_chr13g0396531 | Putative toll/interleukin-1 receptor; leaf ↓ | |
| Novel-mir65 | HannXRQ_chr13g0396531 | Putative toll/interleukin-1 receptor; leaf ↓ | |
| Novel-mir66 | HannXRQ_chr14g0435571 | Auxin-induced protein, leaf ↑ | |
| MiR172a-2 | HannXRQ_chr15g0491641 | Leaf ↑; root ↑ | |
| MiR156a-2 | HannXRQ_chr17g0534011 | (S)-urea glycine amidohydrolase; leaf ↑ | |
| Novel-mir17 | HannXRQ_chr17g0569261 | Probable response regulator 11; root ↓ | |
| miR156 | HannXRQ_chr14g0435381 | SPL; leaf ↑; root ↑ | |
| miR159 | HannXRQ_chr14g0435381 | MYB transcription factor, leaf ↑; root ↓ | |
| miR160 | HannXRQ_chr14g0435381 | ARF; leaf ↑; root ↑ | |
| miR162 | HannXRQ_chr14g0435381 | GTPase activating protein-like; leaf ↑ | |
| miR164 | HannXRQ_chr14g0435381 | NAC domain-containing protein; leaf ↑; root ↑ | |
| miR169 | HannXRQ_chr14g0435381 | CCAAT-box-transcription factor; leaf ↓; root ↑ | |
| miR172 | HannXRQ_chr14g0435381 | APETALA2 transcription factor; leaf ↓; root ↓ | |
| miR319 | HannXRQ_chr14g0435381 | MYB transcription factor; leaf ↑; root ↓ | |
| miR396 | HannXRQ_chr14g0435381 | Heat shock protein; leaf ↓; root ↓ | |
| miR398 | HannXRQ_chr14g0435381 | Cu/Zn superoxide dismutase; leaf ↑; root ↓ | |
| miR482 | HannXRQ_chr14g0435381 | TPG; leaf ↑; root ↑ | |
| miR528 | HannXRQ_chr14g0435381 | Glyceraldehyde-3-phosphate dehydrogenase; leaf ↑; root ↓ | |
| miR838 | HannXRQ_chr14g0435381 | Small heat shock protein (Mds1); leaf ↓ | |

**Triticum aestivum**

[298]
### Table 4. Cont.

| Plant Name | miRNAs | Target | Target Description | References |
|------------|--------|--------|--------------------|------------|
|            | miR1120 | Glyceraldehyde-3-phosphate dehydrogenase; leaf ↑ | | |
|            | miR1169 | Small GTP-binding protein; root ↑ | | |
|            | miR1436 | Glutathione S-transferase; root ↑ | | |
|            | miR1450 | Manganese superoxide dismutase; leaf ↓ | | |
|            | miR2102 | Calmodulin-binding family protein; root ↑ | | |
|            | miR4393 | ARF; leaf ↑; root ↓ | | |
|            | miR4993 | SKP1/ASK1-like protein; root ↑ | | |
|            | miR5048 | RPG1, serine/threonine protein kinase; root ↓ | | |
|            | miR5049 | Wpk4 protein kinase, leaf ↑; root ↑ | | |
|            | miR5059 | Heat shock protein; root ↑ | | |
|            | miR5075 | Serine/threonine protein kinase 3; root ↑ | | |
|            | miR5083 | Hydroxymethylglutaryl-CoA synthase; leaf ↑ | | |
|            | miR5174 | NBS-LRR genes, leaf ↑; root ↑ | | |
|            | miR5175 | Methylene-tetrahydrofolate reductase; leaf ↑ | | |
|            | miR5205 | Malate dehydrogenase, CBS domain-containing protein; leaf ↑ | | |
|            | miR5568 | Pathogenesis-related protein, leaf ↑; root ↓ | | |
|            | miR6108 | Glycosyltransferase; leaf ↑ | | |
|            | miR396a-5p | Superoxide dismutase [Mn] 1, mitochondrial | | |
|            | miR834 | Superoxide dismutase [Fe], chloroplastic-like isoform X2 | | |
| Zanthoxylum bungeanum | miR167a-3p | Peroxiredoxin-2E, chloroplastic (POD) | | |
|            | miR169b-3p | Catalase isozyme 1(CAT) | | |
|            | miR447a-3p | L-ascorbate peroxidase 3 | | |
|            | miR773b-3p | Phospholipid hydroperoxide glutathione peroxidase 1, chloroplastic | | |
|            | miR397b | Delta-1-pyrroline-5-carboxylate synthase, key enzyme for the synthesis of proline | | |
|            | miR397b | JAR1 | Jasmonic acid-amido synthetase (participate in the synthesis of jasmonic acid) | | [14] |
|            | miR859 | ABSCISIC ACID–INSENSITIVE 5-like protein 5, (regulate a variety of ABA responses, such as stomatal closure, plasma membrane permeability and water permeability) | | |
|            | miR5632-5p | Mitogen-activated protein kinase 1 | | |
|            | miR1888a | Protein disulfide-isomerase 5-2 isoform X1 | | |
Table 4. Cont.

| Plant Name | miRNAs       | Target Description                                      | References |
|------------|--------------|----------------------------------------------------------|------------|
|            | miR5638a     | Respiratory burst oxidase homolog protein C (Citrus sinensis) |            |
|            | miR398a-3p   | Probable nucleoredoxin 1                                  |            |
|            | miR3434-3p   | Translationally controlled tumor protein homolog; involved in the regulation of abscisic acid–mediated and calcium-mediated stomatal closure |            |

In *Medicago truncatula*, miR169 was downregulated only in the roots while miR398a,b and miR408 were strongly upregulated in both shoots and roots under drought stress [299].

In a *Populus* plant, miR156, miR159, miR171, miR319, miR395 and miR474 were upregulated in response to drought stress [300]. In *Populus tomentosa*, about 152 conserved miRNAs were identified and the expression of 17 conserved and nine novel miRNAs was investigated in response to drought stress [301]. In *Vitis vinifera*, 12 novel and species-specific miRNA candidates were reported in response to drought stress. Moreover, 70 conserved miRNAs were identified and 28 novel miRNAs were predicted in a drought-resistant grapevine [302].

Differential regulation of miRNAs in response to drought stress has been well studied in maize [253,286,288,302–304]. For example, miR398 was upregulated after treatment with polyethylene glycol and downregulated under soil drought [305]. The downregulation of miR167 during drought stress upregulated its target PLD (Phospholipase D), which is involved in controlling ABA response and stomatal movement [21]. Similarly, the downregulation of miR159 in drought triggered the expression of HD-ZIP, ARF and GA-MYB transcription factors, which contributed to greater adventitious and lateral root formation.

Moreover, miR474 was upregulated in drought to inhibit proline dehydrogenase (PDH) [306], while miR827 was upregulated during drought stress to act on NADP-binding and SPX (SYG1/Pho81/XPR) transcripts to activate stress signal transduction pathways [305].

It was shown that miR156 interacts with the ABA-dependent strigolactone signaling pathways in tomatoes under drought stress. The study identified miR156 as a mediator of stomatal movements and the findings indicated a cause–effect link between miR156 accumulation and regulation of water relations and stomatal functioning [307]. In sugarcane, miR169* was shown to target various transcripts such as *Elongation Factor 1-alpha (EF 1α)* in response to water depletion [297]. It was identified that miR529, miR535 and miR156 regulate transcripts of *Squamosa-promoter binding protein-like* (SPL) to control organ development and morphogenesis during stress. Similarly, miR159 targets MYB33 and miR172 targets AP2 (*Apetala 2*) to regulate plant development in response to drought stress [152].

Functional studies have provided an insight into the role of miRNAs in regulating the response to drought stress. In *Arabidopsis*, overexpression of ath-miR169a [308] and gma-169c [309], which targets the *Nuclear factor Y-A* (NF-Y-A) resulted in increased drought stress sensitivity. In contrast, similar studies in tomatoes have reported that overexpressing sly-miR169c show negative regulation of stomatal movement, reduced leaf water loss and transpiration rate, and improved drought tolerance [310]. Overexpression of Osa-miR393, which targets the auxin-responsive OsTIR1 and OsAFB2, lowered the tolerance of rice plants to salt and drought stress [230]. In another example, Osa-miR319 overexpression in creeping bentgrass led to greater tolerance to salinity and drought, by decreasing the expression of its putative target genes: *AsPCF5, AsPCF6, AsPCF8, AsTCP14*. 
and AsNAC60 [283]. In Populus ussuriensis, overexpression of Pu-miR172d significantly decreased stomatal density by directly repressing the expression of PuGTL1 and PuSDD1. This resulted in increased water use efficiency and drought tolerance by reducing net photosynthetic rate, stomatal conductance and rate of transpiration [311]. This study showed that Pu-miR172d-PuGTL1-PuSDD1 module played an important role in stomatal differentiation and acted as a potential target for creating drought-tolerant plants. Similar studies in other plants showed that overexpression of miR156 in Alfalfa [312], miR408 in chickpea [282], Osa-miR319a in creeping bentgrass [283], miR169 in tomato [310] and miR159 in potato [313] resulted in enhanced drought stress tolerance. Recently, it was shown that miR535 overexpressing and CRISPR/Cas9 knockout rice showed enhanced stress tolerance when tested in presence of sodium chloride, polyethylene glycol, abscisic acid and dehydration stresses parameters [314].

4.3. Interaction between Long and Small ncRNAs in Drought Stress

Studies on the mechanism of action of IncRNAs have revealed their complex interaction with the small ncRNAs. Together, they form complex regulatory hubs for controlling various drought responsive pathways at the transcription, post-transcription and epigenome levels. Studies in Cassava showed that 11 drought-specific differentially expressed IncRNAs acted as target mimics for miR156, miR164, miR169 and miR172 [116]. Under drought stress, lincRNA340 acts as a target mimic of miR169 to enhance the expression of its target gene NFY [115]. The IncRNA, TCONS_00068353 acted as a target mimic for miR156k and miR172c to control several abiotic stress-responsive genes [116].

Many plant TEs contain stress-responsive cis-acting elements and produce IncRNAs in response to specific stress [315], and many of these are possible sources of small ncRNAs that can regulate both TE and non-TE transcripts based on sequence complementarity. In maize, eight drought-responsive IncRNAs acted as precursors of miRNAs [102]. It was shown that TE-derived epigenetically activated siRNAs (easiRNAs) participated in transcriptional silencing. In rice, TE-siRNA815 could induce a de novo DNA methylation process via the RdDM pathway [316]. The stress-downregulated Osa-miR820 originates from CACTA-TE [317] and targets de novo DNA methyltransferase (DRM2) transcripts. Overexpression of Osa-miR820 enhanced salt tolerance in rice plants [318]. It was also shown that ZmNAC111 expression is repressed by miniature inverted-repeat transposable element (MITE) through RdDM and H3K9 dimethylation during drought tolerance [121]. Overexpression of the ZmaNAC111 gene boosted drought tolerance in maize seedlings [319]. This phenomenon has unveiled functional crosstalk between small ncRNAs and the TEs, indicating that novel stress-responsive regulatory networks may be operative in plants [70,320].

5. Conclusions and Perspectives

The steadily increasing world population has challenged the agricultural sector to produce a substantial amount of crops. However, crop productivity all over the world is anticipating challenges by the ever-changing climate, variable weather conditions and environmental stresses. The limited availability of water and global warming has increased the incidence of drought, making it a major contributor to agricultural losses. To tackle this problem and produce enough food to feed the growing world population, it is important to generate crops that can survive underwater limiting conditions and can evade drought stress. This process can be aided by a thorough understanding of plant responses to water deficit and drought stress.

The exciting discovery of RNA-mediated gene silencing has highlighted the role of long and small ncRNAs in maintaining the homeostasis of gene expression. Advances in RNA-Seq analysis, computational analysis and functional genomic studies have enabled the discovery of several long and small ncRNAs and facilitated the understanding of their regulations. However, their functional characterization and annotation are limited to select plant species. Though the studies on ncRNAs are still in their infancy, their discovery has unraveled a novel mechanism of gene regulation. The small ncRNAs, such
as miRNAs, regulate various aspects of plant biology, while the long ncRNAs have a role in regulating the miRNAs by acting as target mimics, sponges or decoys. The ncRNAs normally work in highly complex and intricately connected networks to regulate plant growth and development. The small ncRNAs belong to large families where specific members may be associated with a definite development stage or response.

In the last few years, substantial progress has been made in deciphering the mechanisms of ncRNAs. It has been shown that the small ncRNAs have the ability to move systemically within the plant’s vasculature or locally from one cell to another. This was demonstrated by micro-grafting miR399 overexpressing Arabidopsis shoots on wild-type roots. The chimeric plants accumulated very high levels of mature miR399 species in the wild-type roots, where the primary transcripts were virtually absent. The chimeric plants showed downregulation of PHO2 in the wild-type roots and Pi accumulation in the shoots. This indicated a role for the miRNAs in long-distance signaling for maintaining nutrient balance [321]. The miR399 could not only move through the phloem tissues, but the transported molecules retained their biological activity in the recipient tissues. In another report, both ath-miR399d and its star sequence were identified as the mobile elements. During phosphate starvation, translocation by miR827 and miR2111a between shoots and roots was also demonstrated [322]. The long-distance mobility of miRNA species reflects on their potential in root–shoot communications during stress responses [323,324]. The miRNA shuttles may be operative in response to drought stress, as well. Indications towards this come from studies on gma-miR172, which is induced under salt and drought treatments. The miR172 cleaves/inhibits the transcript encoding AP2/EREBP-type transcription factor (SSAC1) to relieve inhibition of thiamine biosynthesis gene (THI1) that encodes a positive regulator of salt stress tolerance [325].

There is no doubt that the ncRNAs play a crucial role in regulating plant growth and stress responses. Many important issues remain to be answered, such as how do the ncRNAs move from the cells where they are produced and move into the recipient cells? How are the ncRNAs transported, and in what way are they protected from nucleolytic degradation during movement? Are there specific proteins or chemical tags which help them in such transfers?

The information related to long ncRNAs is still emerging, and there is still a lot more to discover with respect to their functions and regulations. Dedicated and systematic efforts will be required to understand how the ncRNAs networks operate in different crop plants over spatiotemporal boundaries and identify their association with response to drought and related stresses. It will be a lot more exciting to understand if they have any role in influencing inter-organ communications and stress responses. In this context, genetic screens and transgenic approaches will aid in unraveling their novel functionalities and features. It is envisaged that such studies will open up opportunities for designing efficient strategies for development of stress-tolerant crops.

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