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Unveiling the biosynthesis, mechanisms, and impacts of miRNAs in drought stress resilience in plants

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ABSTRACT

Drought stress is one of the most serious threats to sustainable agriculture and is predicted to be further intensified in the coming decades. Therefore, understanding the mechanism of drought stress tolerance and the development of drought-resilient crops are the major goals at present. In recent years, noncoding microRNAs (miRNAs) have emerged as key regulators of gene expressions under drought stress conditions and are turning out to be the potential candidates that can be targeted to develop drought-resilient crops in the future. miRNAs are known to target and decrease the expression of various genes to govern the drought stress response in plants. In addition, emerging evidence also suggests a regulatory role of long non-coding RNAs (lncRNAs) in the regulation of miRNAs and the expression of their target genes by a process referred as miRNA sponging. In this review, we present the regulatory roles of miRNAs in the modulation of drought-responsive genes along with discussing their biosynthesis and action mechanisms. Additionally, the interactive roles of miRNAs with phytohormone signaling components have also been highlighted to present the global view of miRNA functioning under drought-stress conditions.

1. Introduction

Drought is one of the major stresses that negatively affects the growth and development of plants and causes extensive crop loss around the globe (Ahmad et al., 2022; Xiangyi Li et al., 2020). Changes in environmental conditions including high temperature, low precipitation, high light intensity, and global warming, among others, are the major reasons for the enhanced frequency of drought stress in recent years (Seleiman et al., 2021). Moreover, the effects of drought on agriculture are further aggravated due to the depletion of water resources and the increased food demand for the rapidly expanding world population (O'Connell, 2017). Drought stress alone can trigger a crop yield loss by up to 11% globally and thus is considered a major threat to food security (Lesk et al., 2016). The depletion of cultivated lands along with drought stress by the end of 2050 is predicted to impact crop production and the quality of food severely (Naumann et al., 2018) (see Figs. 1–3).

Drought stress is known to adversely affect the morphological, physiological, and biochemical aspects of plants (Queiroz et al., 2019; Wahab et al., 2022). In general, drought stress inhibits seed germination due to low water content leading to poor establishment of seedlings (Islam et al., 2018), promotes leaf abscission, and retards cell growth

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(Elnaggar et al., 2018). In addition, drought stress also induces turgor loss, decreased relative water content, stomatal closure, leaf wilting, damage to the plasma membrane, and disturbs key metabolic processes including photosynthesis (Ferrara et al., 2011; Istanbuli et al., 2020). Additionally, the efficiency of Rubisco is greatly inhibited which results in reduced photosynthetic activity and thus overall yield (Wahab et al., 2022). Drought stress also induces the generation of reactive oxygen and reactive nitrogen species, however, the plant antioxidant system is compromised under intensive and prolonged drought conditions, resulting in oxidative damage to the cell membrane and organelles such as chloroplast, mitochondria, and nucleus (Khan et al., 2021b). Therefore, efforts need to be taken up to develop drought-tolerant crops to maximize their yield and to ensure "food for all" in the coming decades.

Drought-tolerant plants, which are often the wild relatives of cultivated plants, activate a sophisticated signaling cascade that culminates into drought tolerance. This drought stress signaling includes post-transcriptional regulation of genes related to drought stress, activation of phytohormones signaling, and biosynthesis of antioxidants and secondary metabolites, among others (Khan et al., 2021a; Riyazuddin et al., 2022). In addition, accumulating evidence also suggests that some of the small single-stranded non-coding RNAs of 20–24 nucleotides play regulatory roles in providing drought stress tolerance in plants (Shriram et al., 2016). Non-coding RNAs are mainly categorized into housekeeping ncRNAs and regulatory ncRNAs based on their origin, biogenesis, and mode of action. Of these, housekeeping ncRNAs include transfer RNAs (tRNAs), small nuclear RNAs (snRNAs), ribosomal RNAs (rRNAs), and small nucleolar RNAs (snoRNA) and are associated with cellular and ribosomal functions in plants and animals while regulatory ncRNAs include short interfering RNAs (siRNAs), piwi interacting RNAs (piRNAs), miRNAs, and long noncoding RNAs (lncRNAs). Based on the biogenesis and their mode of action, siRNAs are further grouped into trans-acting siRNA (tasiRNA), heterochromatic siRNAs (hc-siRNA), and natural antisense siRNAs (nat-siRNAs) (Waititu et al., 2020). Endogenous siRNA synthesis begins with endogenous sequences, including transposons, repetitive elements, or tandem repeats which cleave the target RNA utilizing dsRNAs, DCL enzyme activities, and the RISC-containing AGO protein (Zhang et al., 2023). Jung and co-workers reported that SiRNAs target drought-associated genes including those involved in photosynthesis, antioxidant defense, and proteolysis in drought-tolerant rice plants under drought-stress conditions (Jung et al., 2016; Khraiwesh et al., 2012). However, the involvement of these siRNAs in plant fitness at the molecular, physiological, and biochemical levels is still ambiguous under drought stress.

Among these ncRNAs, microRNAs (miRNAs) are best known to regulate the drought stress response in plants by modulating the expression of various target genes either by silencing or decreasing their transcript levels (Singroha and Sharma, 2019). Emerging evidence indicates that a single miRNA molecule can regulate the expression of a

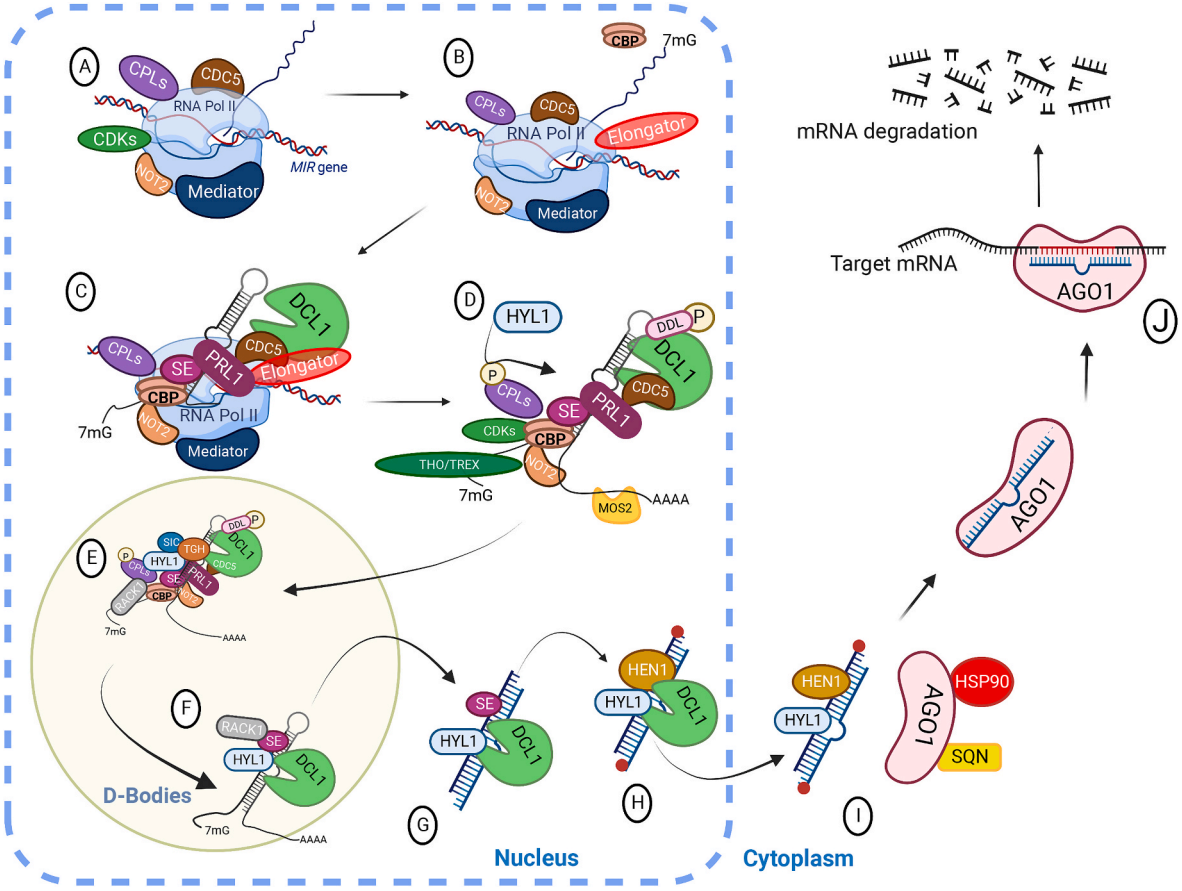

Fig. 1. Figure illustrating the sequential protein positioning during miRNA biogenesis and target mRNA degradation. **(A)** MIR genes are transcribed by RNA Pol. II, which is recruited to the promoter region with the help of NOT2, CDC5, and MEDIATOR. **(B)** recruitment of elongator to the synthesizing pri-miRNA. **(C)** Formation of the hairpin-loop structure by elongating pri-miRNA with 5′ end bounded by CBP and the recruitment of DCL1 and its accessory proteins. **(D)** Processing of pri-miRNA brought about by the crosstalk of NOT2, CDC5, PRL1, DCL1, and SE. The recruited DDL stabilizes the transcribed miRNA and MOS2 and THO/TREX complex mediates the transportation of the complex to D-bodies. **(E–F)** Inside the D-bodies, the DCL1 cleaves the miRNA and results in the formation of a 15–20 nucleotide long miRNA:miRNA* duplex. **(G–H)** Methylation of 3′ end of both the miRNA strands of the duplex and transportation from the nucleus to cytoplasm. **(I)** splitting of miRNA:miRNA* into the guide and passenger strands, with guide strand binding to AGO1. **(J)** Binding of the AGO1 complex with loaded miRNA to the target mRNA based on the sequence complementarity ultimately leading to target mRNA degradation.

considerable number of genes as well as hundreds of mRNAs responsible for governing various cellular processes in plants including growth and development, and responses to biotic and abiotic stress conditions (Sunkar et al., 2012; Waheed and Zeng, 2020). In particular, the expression of drought-responsive genes belonging to the myelo-blastosis (MYB), Nuclear Factor Y (NF–Y), NAM: no apical meristem (NAC), and Homeodomain-leucine zipper (HD-ZIP) class of transcription factors are highly controlled by miRNAs (Sunkar et al., 2012). In addition, miRNAs are also involved in the regulation of genes involved in antioxidant defense and activation of ABA-dependent and/or ABA-independent pathways that are key components of drought stress response in plants. In this review, we describe the regulatory roles of various miRNAs in the regulation of stress response genes and present a putative pathway of miRNA-mediated drought stress tolerance in plants.

2. Biogenesis and processing of miRNAs in plants

miRNAs are synthesized by *MIR* genes and their production is temporally and spatially regulated (Achkar et al., 2016; Cui et al., 2017). During miRNA biogenesis, various regulatory transcription factors such as bHLH and MYB interact with the promoter sequence of *MIR* genes along with RNA polymerase II which results in the formation of nascent pri-miRNA (Achkar et al., 2016). The process of miRNA biogenesis is a series of four consensus biochemical steps including (1) initiation of transcription by RNA polymerase II, (2) elongation and processing of dsRNA, (3) 3 -O-methylation of sRNA, and (4) sRNA incorporation into effector complex to associate with the target mRNA (Voinnet, 2009). All of these steps require a series of additional proteins that govern the process of miRNA biogenesis (Table 1) (Gao et al., 2021; Jeena et al., 2022; Li and Yu, 2021). In the initiation phase, RNA polymerase II is recruited to the promoter with the help of NOT2 (NEGATIVE ON TATA LESS 2), CDC5 (CELL DIVISION CYCLE 5), and MEDIATOR after which the phosphorylation of the C-terminal domain (CTD) of the polymerase is carried out which is regulated by CYCLIN-DEPENDENT KINASES (CDKF1 AND CDKDs) and CPLs (C-TERMINAL DOMAIN PHOSPHATASE). This phosphorylation/dephosphorylation event is required to modulate the activity of RNA polymerase and thus miRNA biogenesis (Rogers and Chen, 2013). The second step of miRNA biosynthesis includes the elongation of pri-miRNA in which the synthesizing single-stranded pri-miRNA forms a double-stranded stem-loop structure. Recent evidence shows that the elongation and processing of the nascent pri-miRNA are closely connected as both of these processes occur simultaneously (Fang et al., 2015). The elongator complex with developing pri-miRNA acts as a scaffold, attracting DICER-LIKE 1 (DCL1) enzyme and its accessory proteins SERRATE (SE) and HYPONASTIC LEAVES (HYL1) which interact with DCL1 for efficient and precise processing of pri-miRNA. The 5′ end of the forming nascent pri-miRNA is bound by the nuclear cap-binding complex (CBC). The processing of pri-miRNA is regulated by the crosstalk of NOT2, CDC5, and PRL1 with DCL1 and SE. The transcribed miRNA is stabilized by DDL (The RNA-binding protein DAWDLE) and transported to D-bodies (Dicing--bodies) via MOS2 (MODIFIER OF SNC1 2) and the THO/TREX complex. Depending on the miRNA, DCL1 starts the processing (cleavage) either from the base or the loop, resulting in the formation of a 15–20 nucleotide-long miRNA:miRNA* duplex. The coordinated signaling of HUA ENHANCER1 (HEN1) with DCL1 and HYL1 displaces SE from the complex and methylates the 3′ end of both the miRNA strands of the duplex with a 2′-O-methyl group. The addition of 2′-O-methylation at 3′end protects the miRNA from the endonuclease activity (Budak and Akpinar, 2015). Following this, the duplex is then transported from the nucleus to the cytoplasm by plant exportin 5 ortholog HASTY transporter (Waititu et al., 2020). The miRNA/miRNA* duplex splits into guide and passenger once it is inside the cytoplasm. The thermodynamic stability of the 5′ end to some extent determines the choice of the guide strand which is loaded into the RNA-induced silencing complex (RISC) through binding with Argonaute (AGO) while the other strand is degraded (Fang et al., 2015; Voinnet, 2009). Additional proteins such as Heat Shock Proteins (Hsp90) are also incorporated in the completely assembled complex (Rogers and Chen, 2013) which is then guided to the target site where miRNA binds to the target mRNA through sequence complementarity. After binding, miRNA either cleaves the target mRNA or inhibits translation (Budak et al., 2015) (see Table 2).

In recent years, some of the lncRNAs have been identified that regulate miRNA biogenesis (Chekanova, 2015). LncRNAs are usually longer than 200 nucleotides and can function as the precursors and regulators of miRNA biogenesis (Kim and Sung, 2012). For instance, a lncRNA, TahlnRNA27, is suggested to be a precursor of Ta-miR2010 as revealed by the secondary structure and respective expression analyses (Xin et al., 2011). TahlnRNA27 was found to contain the Ta-miR2010 family sequences, suggesting it to be its precursor. Moreover, 1 h-long heat treatment induced expressions of both TahlnRNA27 and Ta-miR2010, further suggesting that their expression is interlinked. In addition, using 664 long ncRNAs along with their aligned miRNA precursors, 8 lncRNAs were identified as the precursors of 7 identified

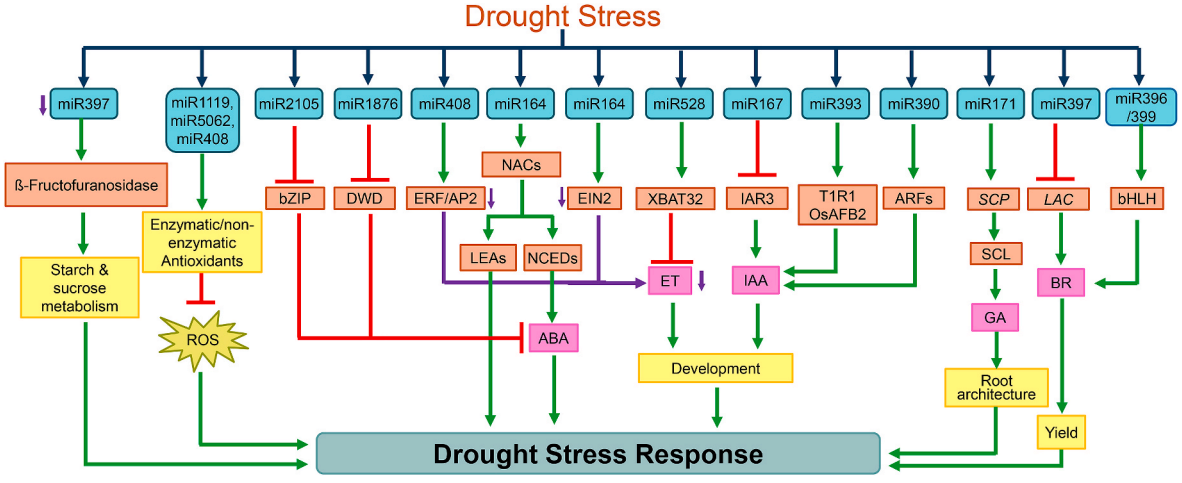

Fig. 2. Involvement of miRNAs in the regulation of phytohormones biosynthesis and signaling under drought stress conditions in plants. Abbreviations: micro-RNA (miRNA); reactive oxygen species (ROS); Basic Leucine Zipper Domain (bZIP); DDB1-binding WD40 protein (DWD); apetala2/ethylene responsive factor (AP2/ERF); NAC (NAM, ATAF and CUC); Nine-cis epoxycarotenoid dioxygenases (NCEDs); Late embryogenesis abundant (LEA); ethylene insensitive 2 (EIN2); IAA-ALA RESISTANT 3 (IAR3); transport inhibitor response 1 (TIR1); Auxin Response Factors (ARFs); Sperm-Coating Protein (SCP); Scarecrow-like (SCL); Laccase gene (LAC1); basic helix–loop–helix (bHLH); Abscisic acid (ABA); Ethylene (ET); Indole-3-acetic acid (IAA); Gibberellic acid (GA); Brassinosteroids (BRs).

maize miRNAs including miR827, miR399b, miR172c, miR169d, miR399e, miR169h, and miR167j (Zhang et al., 2014b). Besides functioning as the precursors for miRNA biogenesis, lncRNAs can also be involved in the transcriptional inhibition of miRNAs by target mimicry. lncRNAs can bind to miRNAs through sequence complementarity, thus inhibiting their effects on target mRNA, a process which is referred to as miRNA decoy, miRNA sponge, or competing endogenous RNA. The mechanism of this miRNA sponging has majorly been studied in animals to date and reports on this mechanism in plants are scanty (Salmena et al., 2011). Yet, some of the recent studies have shown the occurrence of miRNA sponging in Arabidopsis (Franco-Zorrilla et al., 2007) and maize (Salmena et al., 2011) during low Pi tolerance, in tomato during pathogen infection (Cui et al., 2020; Fan et al., 2015; Wang et al., 2015; Yang et al., 2019b), and in cassava (Li et al., 2017) and melon (Gao et al., 2020). In addition, a few lncRNAs have also been identified that are involved in the sponging of miRNAs which regulate the expression of drought-responsive genes or transcriptional factors. For instance, lncRNA MSTRG.42613.1 was shown to be involved in the sponging of miRNA164 which regulates drought stress in *Cleistogenes songorica* (Jha et al., 2020). However, more such reports are required to fully understand the mechanism of lncRNAs-based miRNA sponging and their role in drought stress response in plants.

3. Mechanism of action of miRNAs

It is now well established that miRNAs regulate various physiological processes in plants, however, the molecular mechanism of their functions is not well understood. Accumulating evidence indicates that miRNAs can target multiple genes and regulate their expression through different mechanisms of which the cleavage of the target transcript, is one of the major employed mechanisms. During cleavage of the target genes, miRNAs, after their biogenesis, are transported to the cytoplasm where they bind to the target mRNAs based on specific sequence complementarity, forming a double-stranded RNA (dsRNA) (Fahlgren and Carrington, 2010). The RNA-induced silencing complex (RISC), loaded with Argonaut (AGO1), identifies the dsRNA and cleaves it to repress the translation of the transcribed target gene (Baumberger and Baulcombe, 2005; Waititu et al., 2020). Studies have shown that AGO1 of the complex, with two of its signature domains- PIWI and PAZ similarly show cleavage properties as RNase-H (Baumberger and Baulcombe, 2005; Rivas et al., 2005). The higher the degree of complementarity between miRNA and target mRNA, the higher the effective target splicing (Mallory et al., 2004).

In addition to the cleavage, some other mechanisms such as translational repression and de-adenylation of the target gene are also employed by miRNAs to regulate the expression of their target genes (Rhoades et al., 2002). However, these mechanisms are usually preferred if there is limited complementarity between miRNAs and their target genes or when the catalytic activity is missing from AGO proteins (Braun et al., 2012). Of these, only translational repression has been observed in plants while reports on the de-adenylation of the target gene have been reported in animals. In plants, de-adenylation is missing because of the absence of GW182 protein orthologs which play key roles in the de-adenylation process (Tyagi et al., 2019). Translational

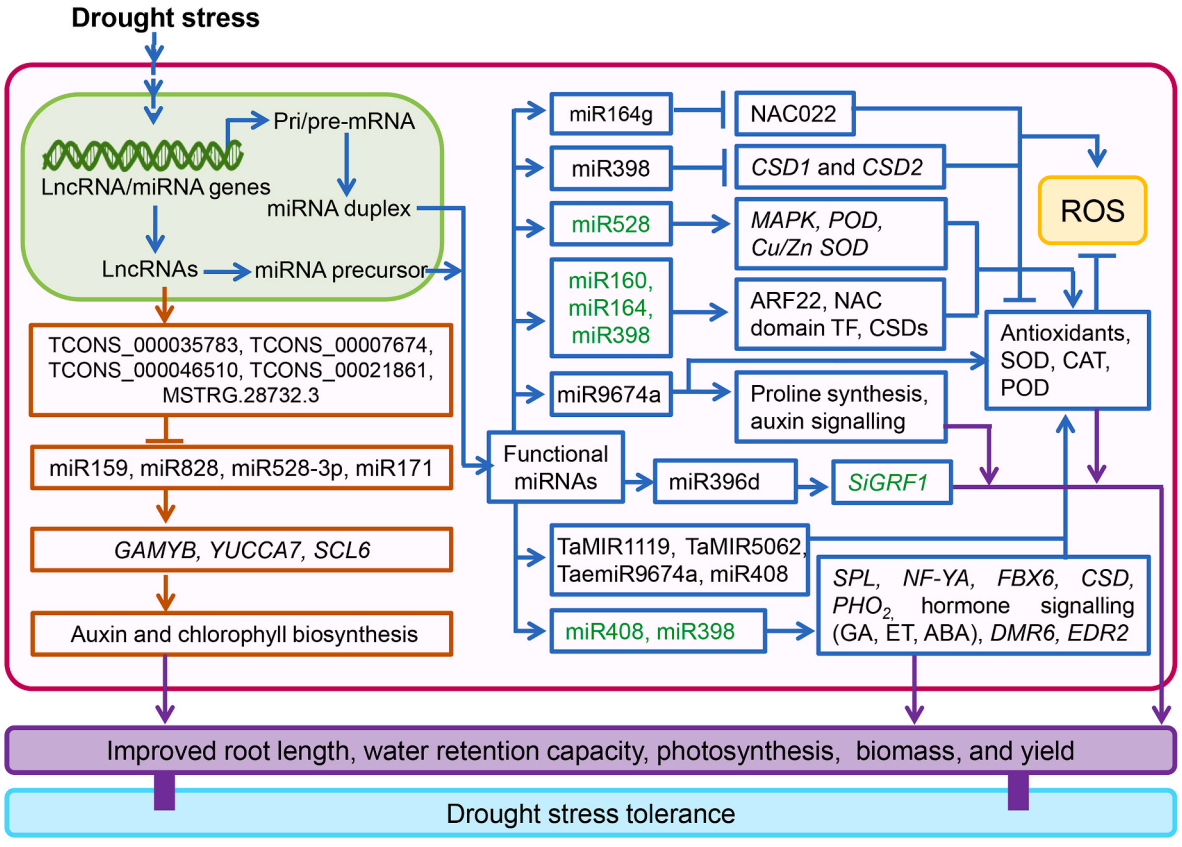

Fig. 3. Schematic representation of the putative mechanism of miRNAs in the regulation of drought stress tolerance in plants. miRNAs highlighted by green color are negative regulators of the drought stress tolerance in plants. Abbreviations: MicroRNA (miRNA); No apical meristem protein (NAC); Cu/Zn-SODs (CSDs); mitogen-activated protein kinase (MAPK); peroxidase (POD); superoxide dismutase (SOD); catalase (CAT); auxin response factor (ARF); growth-regulating factor (GRF); reactive oxygen species (ROS); squamosa promoter-binding-like protein (SPL); Nuclear Factor Y (NF–Y); myeloblasts (MYB); F-box only protein 6 (FBX6); phosphate 2 (PHO_2); gibberellic acid (GA); ethylene (ET); abscisic acid (ABA); downy mildew resistance 6 (DMR6); enhanced disease resistance 2 (EDR2); long non coding RNA (LncRNA); gibberellin- and abscisic acid-regulated MYB (GAMYB); Tryptophan aminotransferase of Arabidopsis (TAA)/YUCCA (YUCCA); scarecrow-like protein-SCL6 (SCL6).

Table 1
List of proteins facilitating miRNA biogenesis.

Biosynthesis step	Protein name	Function	Reference
Initiation	RNA polymerase II	Polymerase activity; involved in the addition of ribonucleotides complementary to the template strand	Kim et al. (2011)
	NOT2 (NEGATIVE ON TATA LESS 2)	Assist in the association of RNA polymerase II to form the initiation complex	Wang et al. (2013)
	CDC5	Interacts with both RNA Pol II and Dicing complex and is required for miRNA biogenesis	Rogers and Chen (2013)
	CPLs (C-TERMINAL DOMAIN PHOSPHATASE-LIKE1)	Required to maintain the hypophosphorylated state of HYL1; is recruited to the DCL1 complex by SE, where it regulates HYL1 function through dephosphorylation	Manavella et al. (2012)
	CDKs (CDKF1 and CDKD)	Regulate Phosphorylation of Serine Residues in the C-Terminal Domain of Arabidopsis RNA Pol II	Hajheidari et al. (2012)
	Mediator Complex	General transcriptional coactivator of Pol II; promotes Pol II transcription	Kim et al. (2011)
Elongation and processing	CBP20 and CPB80 (Cap-binding protein)	Forms a heterodimeric complex with the 5′ cap structure of primary transcripts to perform three functions: transcript stability, splicing efficiency, and 3′ end formation	Kim et al. (2008)
	Elongator complex	Interacts with the DCL1-containing Dicing complex and functions in both transcription and processing of pri-miRNAs and couples these two processes	DeFraia and Mou (2011)
	DCL1	Precisely excise the miRNA from its precursor	Liu et al. (2012)
	Serrate (SE)	Binds to pri-miRNA and promotes the accuracy of pri-miRNA processing by DCL1	Dong et al. (2008)
	PLEIOTROPIC REGULATORY LOCUS 1 (PRL1)	Interacts with DCL1 and pri-miRNAs and enhances pri-miRNA processing potentially by stabilizing the processing complex	(Zhang et al., 2014a)
	HYPONASTIC LEAVES1 (HYL1)	Interacts with DCL1 for efficient and precise processing of pri-miRNA; required for microRNA accumulation	(KURIHARA et al., 2006; Vazquez et al., 2004)
	THO/TREX	Transport the pri-miRNA to the D-bodies	Francisco-Mangilet et al. (2015)
	The RNA-binding protein DAWDLE (DDL)	The transcribed pri-miRNA is stabilized by DDL upon dual interaction with a putative phosphorylated domain of DCL1 and the transcript	Yu et al. (2008)
	MODIFIER OF SNC1, 2 (MOS2)	Required for efficient pri-miRNA processing and for the association of pri-miRNAs with HYL1	Wu et al. (2013)
Transportation to D-bodies for co-transcriptional processing of pri-miRNAs	G-patch domain protein TOUGH (TGH)	Binds single-stranded RNA; enhances DCL1 activity in pri-miRNA processing; influences the ability of HYL1 to associate with RNA	Ren et al. (2012)
	Pro-rich protein SICKLE (SIC)	Required for the accumulation of mature miRNAs and colocalizes with HYL1 foci	Zhan et al. (2012)
	RECEPTOR OF ACTIVATED C KINASE 1 (RACK1)	Interact with SE to direct the processing of some pri-miRNAs; is also part of the AGO1 complex both in the cytoplasm and the nucleus	Speth et al. (2013)
Transportation from the nucleus to the cytoplasm	HUA ENHANCER1 (HEN1)	Interacts with DCL1 and HYL1 to displace SE from the complex; The 3′ termini of both miRNA strands in the duplex are then 2’ -O-methylated	Baranauskė et al. (2015)
	HASTY transporter	Transportation of the miRNA:miRNA* duplex from the nucleus to the cytoplasm	Waititu et al. (2020)
RNA-induced silencing complex (RISC)	ARGONAUTE1 (AGO1)	Exhibits slicer activity/Target cleavage; translational inhibition activity of plant miRNAs	(Rogers and Chen, 2013; Brodersen et al., 2008)
	SQUINT (SQN)	Associated with passenger strand removal	Iki et al. (2012)
	Heat Shock Protein - HSP90	Chaperone activity may trigger AGO1 conformational changes upon its binding to, or disassociation from, AGO1	Iki et al. (2012)
	SMALL RNA DEGRADING NUCLEASE (SDN1)	Possesses 3′–5′ exoribonuclease activity against short, single-stranded RNA substrates	Ramachandran and Chen (2008)
	HEN1 SUPPRESSOR1 (HESO1)	A nucleotidyltransferase that adds 3′ oligouridylate tails to unmethylated miRNAs; along with SDN1 cooperates in the degradation of methylated miRNAs, with HESO1 acting on a 3′-truncated miRNA generated by the initial removal of the 2′-O-methylated nucleotide by SDN1	(Ren et al., 2012; Zhao et al., 2012)

inhibition is brought about by the imperfect binding of miRNAs to the target mRNAs and is mediated by AGO1 and AGO10. In the absence of perfect binding, AGO recruits GW182 analog protein, termed SUO which encodes GW (glycine and tryptophan) repeat protein necessary for miRNA-mediated translational repression (Yang et al., 2012). This RISC-AGO1 complex binds to the 5’untranslated region (UTR) of the target genes which blocks the ribosome binding sites and thus inhibits their translation (Iwakawa and Tomari, 2013). Other factors such as ALTERED MERISTEM PROGRAM 1 (AMP1), VARICOSE (VCS), GW-repeat protein, and microtubule enzyme KATANIN (KTN1) are also involved in the regulation of the translation inhibition process. Of these, AMP1 aids in the exclusion of miRNA target mRNA from membrane-bound polysomes while GW-repeat protein directly interacts with the PIWI domain of AGO proteins within the RISC complex (Li et al., 2013; Rogers and Chen, 2013). Although both AGO1 and AGO10 are involved in this inhibitory mechanism, it is yet unknown how each AGO gene specifically functions and further research is still required to understand the exact mechanism of miRNAs-mediated translational inhibition in plants (Waititu et al., 2020).

miRNA-directed DNA methylation is another method by which miRNAs regulate the expression of target genes (Waititu et al., 2020). The majority of DNA methylation acts on cytosines with the help of methyltransferases that add a methyl group to the cytosine pyrimidine ring at the 5’ position to induce epigenetic modification and regulate gene expression (Chan et al., 2005). In contrast to traditional cleavage or translational repression, long (23–27 nt) miRNAs generated by DCL3, are involved in inducing the DNA methylation both at cis- and trans-positions of the target gene loci by linking with the AGO4 protein (Jia et al., 2011). Heterochromatic small interfering RNAs are a different class of DCL3-dependent small RNAs that are generated in the nucleus and packed into AGO4 in the cytoplasm before being imported into the nucleus, where they function in RNA-directed DNA methylation. Similar

Table 2
Role of miRNAs in drought stress tolerance.

miRNA	Plant Species	Target	Outcomes	References
miR528	*Zea mays*	MAPK, POD, Cu/Zn SOD	Drought tolerance by inducing stomatal movement and antioxidant defense system	Wei et al. (2009b)
miR395	*Arabidopsis thaliana* and *Oryza sativa*	enzyme ATP sulfurylase	Adaptive response to stress by catalyzing the reaction of inorganic sulfate assimilation	Khraiwesh et al. (2012)
miR393	*Oryza sativa*	TIR1 protein (an F-box protein important for phytohormone auxin signaling)	Downregulate auxin signaling and inhibit plant growth and development during drought conditions,	Lu and Huang (2008)
miR160, miR164, and miR398.	*T. aestivum*	ARF22, NAC domain transcription factor, CSDs	Lower transcript of miRNA under drought leads to the accumulation of the target transcript, leading to the higher activity of SOD, POD, APX	Qiu et al. (2018)
miR1876	*Oryza sativa*	DWD (DDB1 binding WD40) a protein,	Promote ABA signaling in roots by negatively regulating DWD protein	Bakhshi et al. (2016)
miR160	*Arabidopsis thaliana*	ARF10, ARF16 and ARF17	Promote root growth and development via auxin signaling	Singh et al. (2020b)
miR397	*O. sativa* and *Arabidopsis thaliana*	BR-related gene *OsLAC*	Upregulation of miRNA leads to improve grain yield under oxidative stress	Ahmad et al. (2022)
miR159	*Arabidopsis thaliana*	Squamosa Promoter Binding Protein-Like (SPL)	Overexpression of miRNA helps to increase lateral root number under drought	Ranjan et al. (2022)
miR165/166	*Zea mays*	HD-ZIP IIIs	Provide drought tolerance via ABA signaling	T. Yang et al. (2019)
miR474	*Zea mays*	Proline dehydrogenase (PDH)	Upregulation of miRNA promotes Osmo-protection response via proline accumulation	Wei et al. (2009b)
miR408	*Oryza sativa*	OsUCL8 (a plastocyanin-like protein)	Improve photosynthesis and grain yield during drought.	Mutum et al. (2016)
miR169a	*Arabidopsis*	NFY (Nuclear Factor Y)	Provide drought tolerance by regulating antioxidant enzymes such as SOD, GT, and peroxidases	Singroha et al. (2021)
miR395	*Malus domestica*	WRKY33	Provide drought tolerance by cleaving the WRKY33 transcription factor	Niu et al. (2019)
miR169	*S. lycopersicum*	NAC genes	Control leaf water loss and stomatal opening under the drought condition	Tang et al. (2022)
miR169c	*Arabidopsis thaliana*	nuclear factor Y–A (NF-YA)	Overexpression of the miRNA enhances drought stress sensitivity	Yu et al. (2019)
miR1119	*T. aestivum*	bHLH (basic helix–loop–helix), LZ (leucine zipper), and CS (CTP synthase)	Overexpression of miRNA improves ROS homeostasis by promoting antioxidant enzymes such as SOD, CAT, and POD and enhances drought resistance	SHI et al. (2018)
miR156	*Medicago sativa*	Tryptophan-aspartic acid (W-D) repeats (WD 40)	Control leaf water loss and improve root growth during drought	Arshad et al. (2018)
miR396a	*Arabidopsis thaliana*	Growth-regulating factor (GRF)	Overexpression of miRNA reduces stomata density under drought conditions	Liu et al. (2008)
miR167	*Zea mays*	Phospholipase D (PLD)	Downregulation of miRNA promotes stomatal closure via PLD accumulation under drought condition	Wei et al. (2009b)
miR171	*Oryza sativa*	SCL6-I and SCL6-II	Overexpression significantly controls the expression of flavonoid biosynthesis genes via the suppression of *SCL6* gene expression	Um et al. (2022)
miR1916	*Solanum lycopersicum*	Histone deacetylases (HDAC) and strictosidine synthase (STR)	miR1916 negatively regulates the expression of putative target genes HDAC and STR. Therefore, silenced-miR1916 transgenic plants showed higher survival rates	Chen et al. (2019)
miR166	*Camellia sinensis (L.) O. Kuntze*	HD-Zip III	miRNA inhibits the transcription of their putative target by transcript cleavage mechanism and regulates downstream signaling to provide stress tolerance	Tian et al. (2022)
miR408	*Oryza sativa*	Plantacyanins (OsUCL6,7,9 and 30) and pirin	Overexpression of miRNA in drought-sensitive cultivar showed higher vegetative growth with an improved electron transport rate (ETR) and effective photochemical quantum yield of photosystem II (Y(II)) under drought stress	Balyan et al. (2022)
miR166a	M. truncatula	HD-Zip III TF	Overexpression impacts main and lateral roots and controls the number of lateral roots in drought conditions.	Boualem et al. (2008)
miR398	M. truncatula	Cytochrome C oxidase subunit V (COX5b)	Upregulation of miRNA significantly regulates respiration pathways such as mitochondrial respiration under drought	Trindade et al. (2010)
miR156d	*G. hirsutum*	*GhSBP3*	Improve physiological processes such as fiber elongation and secondary wall formation.	Sun et al. (2019)

mechanisms are probably used by miRNAs carrying AGO4 to cause cytosine methylation which regulates the expression of target genes (Law and Jacobsen, 2010; Rogers and Chen, 2013; Ye et al., 2012).

4. miRNAs-mediated regulation of drought stress response

Linear non-coding RNAs consist of miRNAs and long noncoding RNAs (lncRNAs) and are involved in the regulation of growth, development, and stress response by regulating the gene expression at transcriptional as well as post-transcriptional levels (S. Li et al., 2022; Mattick, 2005). In the majority of the cases, miRNAs target their genes and negatively regulate their expression while lncRNAs competitively bind to the complementary miRNAs to regulate the transcript level of target genes (Carrington and Ambros, 2003; Guttman and Rinn, 2012).

In recent years, various conserved miRNAs have been identified in plants that regulate the expression levels of plant-specific transcription factors including growth-regulating factor (GRF), bHLH, and WRKYs, among others, that are the key signaling components of the drought stress response (Jones-Rhoades et al., 2006). A recent study utilizing a transcriptome analysis of foxtail millet, *Setaria italica,* revealed upregulation of a miRNA belonging to the miR396 family *"SimiR396d"* and downregulation of various *SiGRFs* genes under polyethylene glycol (PEG)-induced drought stress in both roots and shoots. Overexpression of *SimiR396d* in *S. italica* resulted in the development of longer roots which improved drought stress tolerance of transgenic plants. In contrast, *SimiR396d* knock-down mutant plants showed dwarf roots and

were drought sensitive. Further, the introduction of target mimics of SimiR396d (MIM396) in the *SimiR396d* overexpression lines improved the transcript levels of *SiGRF1*, indicating *SiGRF1* is a direct functionally relevant target gene of *SimiR396d*. These results suggested that the SimiR396d positively regulates root growth and drought tolerance by maintaining the expression of *SiGRF1* (Zhang et al., 2023).

ZAT5 proteins are Cys2/His2 (C2H2)-Type Zinc finger transcription factors (ZFP), however, their role in drought stress response is not well established. A recent RNA-seq-based transcriptome analysis of apple plants showed an upregulation of *MdZAT5* under drought stress conditions, indicating its potential role in drought stress response (GENG et al., 2019). To further establish the role of MdZAT5 in drought stress, its potential interactors were identified using a yeast two-hybrid (Y2H) approach which showed an interaction between MdZAT5 and cis-elements region of HYPONASTIC LEAVES1 (MdHYL1/DRB1) promoter, a key regulator of miRNA biogenesis that participates in the processing of pri-miRNAs into mature miRNAs (Bao et al., 2022; Lian et al., 2013). Further analysis showed that MdZAT5 interacts with different regions of the *MdHYL1* promoter, for instance, it binds to the a, b, c, and e regions of *MdHYL1* under normal conditions while it interacts with the d and e segments under drought stress conditions. Accumulating evidence has shown that miRNA biogenesis can be promoted by MdZAT5 which encourages the availability of pri-miRNA on the DCL1 complex to enhance the miRNA biogenesis under drought stress while opposite results were obtained under normal conditions potentially because of the presence of diverse binding sites of ZAT5 in the promoter region of *MdHYL1* gene (Bao et al., 2022; Shen et al., 2022). In addition, MdZAT5 can also directly bind to the promoter region of genes associated with ROS-detoxification such as *MdRHA2a, MdLEA14, MdCAT3,* and *MdAPX1* to stimulate the ROS scavenging to promote drought resilience (Bao et al., 2022).

In maize, gene expression data showed the downregulation of a *ZmmiR408a* in response to drought stress, indicating its putative role in the regulation of drought stress response. miR408a knockout maize plants exhibited significantly reduced MDA levels and improved seed germination and overall plant morphological characters such as root length, survival rate, dry mass, seed set rate, crop yield, and seed vigor as compared to wild type and miR408a overexpressing maize lines, indicating a negative role of *ZmmiR408a* in drought tolerance (Jiao et al., 2022). Further, an integrated miRNA–mRNA analysis under drought stress revealed that the majority of the miRNAs targeted genes are associated with the phenylpropane biosynthesis, glutathione metabolism, and starch and sucrose metabolism pathways in the maize roots (Jiao et al., 2022; Kang et al., 2021; Yang et al., 2021). In the case of grapevines, a total of 487 known and 892 novel miRNAs were identified in drought-sensitive and drought-tolerant varieties under drought stress. The drought-tolerant variety exhibited a reduced expression of miR398a/b while it was increased in the sensitive variety during drought-stress conditions. The expression of another miRNA, miR169v/d, was significantly higher in the tolerant variety while another one, miR169a/e/f, was downregulated in both tolerant and sensitive varieties. This differential expression of these miRNAs may regulate different target genes in these grapevines, however further studies are required to reveal the mechanism of how miR169v/d alleviate drought stress in the tolerant variety. The target genes of miR398a/b including those encoding for transcription factors, enzymes, and various types of functional proteins such as squamosa promoter-binding-like protein *(VvSPL)*, nuclear factor-Ys *(VvNF-YA)*, F-box only protein 6 *(VvFBX6)*, Cu/Zn-SOD *(VvCSD)*, PHOSPHATE2 *(VvPHO2)*, hormone signaling pathways, GA, ET, and ABA required for various cell functions. As drought stress reduced the expression of this miR398a/b in the tolerant variety, the cleavage of its target genes was inhibited, resulting in their expression that helped in the alleviation of drought stress (Guo et al., 2023). Along with grapevine, *Camellia oleifera* plants also showed reduced expression of miRNA398 and miR408, however, their target genes identified included downy mildew resistance 6 (DMR6) and enhanced disease resistance 2 (EDR2) that are known to regulate drought response in plants. Taken together, these results suggest that the downregulation of miR398b and miR408 during drought stress conditions subsequently improves the mRNA level of their target genes to improve drought stress tolerance by activating the phytohormones, antioxidant defense, and other drought stress-associated signaling pathways (He et al., 2022).

In *Agropyron mongolicum*, five miRNAs including osa-miR444a-3p.2, bdi-miR408-5p_1ss19TA, taemiR9774_L-2R-1_1ss11GT, ata-miR169a-3p, and bdi-miR528-np3_2ss15TG20CA were identified that target drought-associated genes such as *MADS47T*, *CCX1*, *carC*, *PAO2,* and *HOX24* that are involved in the regulation of brassinosteroid (BR) mediated signaling pathway, Na^+/K^+ transport, hydrolase activity, and oxidation–reduction process, respectively (Fan et al., 2022). Similarly in *Dendrobium huoshanense* and grapevine, a miR156 was identified that targets *SQUAMOSA-promoter binding protein-like (SPL)* and *VvSBP8, VvSBP13*, respectively that regulate the development of lateral roots under drought stress conditions. Drought stress results in the enhanced expression of *miR156* which consequently decreases the expression of its target genes *SPL*, *VvSBP8,* and *VvSBP13,* causing a delay in the developmental process which potentially increases the drought stress tolerance by temporarily arresting the growth to evade the drought stress conditions (Guo et al., 2023; Wang et al., 2021).

Accumulating evidence also highlights the importance of lncRNAs in the regulation of drought stress response in plants via competing with miRNAs and subsequently regulating the mRNA level of target genes by the formation of lncRNA-miRNA-mRNA regulatory networks. In Arabidopsis, approximately 37,000 lncRNAs have been identified and characterized and such identification has also been initiated in other crops such as maize, rice, cotton, canola, tomato, sunflower, *M. truncatula*, *P. tomentosa*, *P. trichocarpa* (Deniz and Erman, 2017). Genome-wide screening and characterization of these lncRNAs elucidated their role in regulating transcription, splicing, RNA-mediated DNA methylation and epigenetic function, flowering, seedling photomorphogenesis, and biotic and abiotic stress response. Similarly, 535 drought-responsive lncRNA were reported and characterized in the roots of drought-tolerant and drought-sensitive genotypes of barley that were associated with hormone signal transduction, diterpenoid biosynthesis, and ascorbate/aldarate metabolism. Among these identified lncRNAs, 10 were exclusively identified in drought-tolerant genotype. Based on the regulatory roles of these identified lncRNAs, the underlying mechanism of drought tolerance in tolerant genotype was proposed which involves lncRNAs-mediated regulation of serine/threonine protein kinase-SMG1, which is involved in mRNA surveillance by acting on helicase up-frameshift 1 (UPF1) for the degradation of mRNA. Drought stress leads to an accumulation of large amounts of abnormal mRNAs that contain premature translation termination codons which hinder the expression of mRNA of drought stress-related genes involved in proline metabolism, ABA signaling, and drought stress-related transcription factors in both drought tolerant and susceptible barley genotypes. Under drought stress, the up-regulated SMG1 acts on UPF1 in tolerant genotype could effectively eliminate these abnormal mRNAs and provide drought tolerance (Qiu et al., 2019). Similar analysis has also been carried out in other plants such as tea where a total of 132 lncRNAs were identified under drought stress conditions as putative endogenous target mimics for 187 miRNAs associated with 136 distinct mRNAs. Among them, TCONS_00035783, TCONS_00007674, and TCONS_00046510 lncRNA were identified as target mimics for stress-responsive and gibberellic acid signaling associated GAMYB-like transcription factor. This GAMYB-like transcription factor plays a key role in drought alleviation; however, its expression is negatively regulated by miR159 and miR828. During drought stress, these lncRNAs acting as target mimics for both of these miRNAs are expressed and regulate their expression by miRNA sponging to allow the expression of GAMYB for drought stress resilience (Baruah et al., 2021).

Competing endogenous RNA (CeRNA) are relatively newly identified

members of the non-coding RNAs which finetune the miRNAs-mediated regulation of genes associated with growth development and drought stress response in plants. The CeRNA concept was given by Salmena in 2011 and described as a competitor of mRNA which compete to bind with miRNA (Salmena et al., 2011). There are several studies speculating the role of lncRNAs as ceRNAs that inhibit miRNA function and thus regulate developmental processes under abiotic stress. In rice, a total of 40 drought-responsive lncRNAs, 23 miRNA, and 103 mRNA were identified, based on which a ceRNA network was developed. A TCONS_00021861 lncRNA was identified as a competing target for miR528-3p with YUCCA7, which is involved in auxin biosynthesis under drought stress. Therefore, by sponging miR528-3p, TCONS_00021861 could modulate YUCCA7 which in turn can activate IAA biosynthesis and impart drought stress tolerance in rice (Chen et al., 2021). Likewise, 16 drought-responsive lncRNAs were identified in Shanlan upland rice that were upregulated under drought stress and had the same target gene Os05g0586700, involved in plant membrane repair under drought stress. Interestingly, one of the 16 lncRNAs identified, MSTRG.28732.3 lncRNA, showed a negative correlation with miR171 and a positive correlation with scarecrow-like protein-SCL6, which negatively regulates chlorophyll biosynthesis. The study concluded that SCL6 inhibits chlorophyll biosynthesis in rice and is affected by MSTRG.28732.3 under drought stress, elucidating lncRNA-miRNA-mRNA mediated drought stress response (Yang et al., 2022). Additionally, two novel miRNAs, miR340 and miR417, were identified in wheat that target the differentially expressed lncRNA (DELs) and DEGs in drought-tolerant and susceptible wheat varieties and promote drought stress tolerance. This was an unusual observation where miRNAs were shown to target the lncRNAs to initiate the unmasking of their target drought-associated genes to potentially improve drought stress tolerance. It was reported that MSTRG.56120.4 lncRNA inhibits the expression of *TraesCS5D02G032189*, *TraesCS1B02G061200*, *TraesCS1A02G003100*, and *TraesCS2B02G0*26700 by activating miR340 in drought-sensitive variety whereas drought tolerant variety utilizes MSTRG.188250.2 lncRNA to activate the miR340, leading to the downregulation of *TraesCS7B02G476700*, which is involved in long and short distance water transportation in plants (N. Li et al., 2022). Conclusively, these results suggest that drought stress response in plants is tightly regulated and is governed by the interaction among lncRNA, miRNA, and mRNA. Despite the current research, more studies are required to fully understand and identify and characterize these non-conserved long non-coding RNAs to fully exploit them for the generation of drought-resilient crops.

5. miRNA-mediated detoxification of drought stress-induced ROS

Drought stress results in the overproduction of ROS which cause membrane damage, ultimately affecting cellular metabolism including photosynthesis, which is a major cause of yield loss (Razi and Muneer, 2021). Interestingly, a growing body of evidence indicates an active role of miRNAs in managing drought stress-induced ROS (SHI et al., 2018). For instance, a wheat miR1119 was found to be upregulated and was involved in mitigating the adverse effects of drought stress by cleaving the transcripts of the genes involved in transcriptional regulation (*TabHLH49* and *TaLZ*), metabolism (*TaPCF* and *TaCS*), and oxidative stress (*TaGT*). Overexpression of *TaMIR1119* showed improved drought tolerance in transgenic tobacco lines along with increased plant biomass, improved photosynthetic parameters, osmolyte accumulation, and enhanced ROS-detoxification because of the elevated activities of antioxidant enzymes including superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD) (SHI et al., 2018). Likewise, heterologous expression of another wheat miRNA, *TaMIR5062*, in tobacco showed better drought tolerance owing to the enhanced activity of antioxidant enzymes such as SOD, CAT, and POD. The upregulation of the miRNA under drought stress modified the transcript of the target genes of antioxidant enzymes, thus, elevating cellular antioxidant efficiency as well as improving water retention capacity by regulating stomata conductance (Qiao et al., 2021). A recent report showed that the overexpression of yet another wheat miRNA, *Tae-miR9674a*, in tobacco showed osmotic stress tolerance by modulating the stomatal movement and ROS homeostasis by increasing the expression of *NtFeSOD, NtCAT1,* and *NtPOD4* genes associated with ROS-detoxification and *NtP5CS1* associated with proline synthesis (Wang et al., 2022). Recently, a drought stress-induced miRNA, miR408, was identified in the Arabidopsis, chickpeas, and rice (Hang et al., 2021). Therefore, in an attempt to understand the function of miR408 in drought stress response in forage crop-perennial ryegrass, heterologous expression of rice *Os-miR408* in *Lolium perenne* (perennial ryegrass) was studied. Transgenic plants performed better under drought stress and exhibited better water retention capacity, lower lipid peroxidation, and reduced electrolyte leakage along with better antioxidant enzymes as compared to the wild-type, indicating a positive role of miR408 in drought stress tolerance (Hang et al., 2021). However, further research is required to identify its target genes and miR408-mediated drought stress resilience.

Various other miRNAs have also been identified that are involved in the regulation of genes associated with the ascorbate-glutathione cycle. Recently, an *in silico* analysis was carried out which revealed that miRNAs such as miR156, miR6445, miR167, miR171, miR390, and miR159 target and regulate the transcript levels of *RcAPX5*, *RcMDHAR2*, *RcDHAR2,* and *RcGR1* in *Ricinus communis*. Among these, drought stress enhanced the expression of *RcAPX3*, *RcMDHAR1*, and *RcDHAR2* in both leaves and roots (Jardim-Messeder et al., 2022). In Arabidopsis, ath-miR447a-3p was shown to target the *APX3* gene and inhibit its function under normal growth conditions, however, under drought stress, reduced expression of this miRNA was reported that leads to an increased level of *APX3* (Fei et al., 2020). A similar negative relation between various other miRNAs and other antioxidant genes has also been reported such as *GPX1* which is targeted by ath-miR773b-3p, *CAT* targeted by ath-miR169-3p, and *SOD* targeted by ath-miR834. During drought stress, plants are known to downregulate the expression of these miRNAs to enhance antioxidant defense to detoxify the stress-induced ROS (Fei et al., 2020). In rice, miR398 targets copper superoxide dismutase (*CSD1* and *CSD2*) and exhibits a differential expression profile in drought-resistant and drought-sensitive varieties (Cheah et al., 2015). The expression level of *osa-miR398b* was found to be lower in the drought-tolerant variety as compared to the sensitive one which led to the accumulation of the target transcripts associated with antioxidant defense and helped in ROS detoxification, thus allowing the plants to mitigate drought stress conditions. Another miRNA, osa-miR528-5p, known to target *APX* in rice and *POD* in maize, was found to be lowered in drought-tolerant rice variety than the susceptible one under drought stress (Cheah et al., 2015; Wei et al., 2009a). These results suggest that miRNAs keep a check on the expression of various genes associated with ROS detoxification under normal conditions and their reduced expression during drought stress allows enhanced expression of these genes to facilitate ROS-detoxification and to minimize oxidative stress-induced injuries.

In addition to the ascorbate-glutathione cycle-associated genes, miRNAs are also known to regulate the expression of other genes that indirectly regulate the ROS-homeostasis in plants. For instance, recently Peng et al. (2022) identified a miR164g that cleaves the transcripts of the MsNAC022 transcription factor in wild apples which is involved in enhancing the expression and activities of ROS-scavenging enzymes. Overexpression of *MsNAC022* in apples showed higher drought tolerance and a healthier root system along with high water content in leaves of transgenic lines as compared to the wild types. Furthermore, the level of H_2O_2 detected in the transgenic plants was reported to be lower due to higher levels of antioxidant enzymes (SOD, POD, CAT), indicating better ROS scavenging activity in transgenic apple than wild types (Peng et al., 2022). Likewise, overexpression of another miRNA, miR1916, reduced the drought stress tolerance in tomato due to lower levels of the Histone

deacetylase (HDAC) and Strictosidine synthase (STR) transcripts that are considered as key regulators of drought stress tolerance in plants. These results indicate that miR1916 acts as a negative regulator of drought stress tolerance (Chen et al., 2019). In the case of tea, a csn-miR398a-3p-1 was identified which cleaves the Cu/Zn-SODs (CSDs), indicating the regulatory role of the miRNA in the direct regulation of SODs expression (Zhou et al., 2019). Similar observations were also reported in other plants such as rice (Lu et al., 2011), tomato (Candar-Cakir et al., 2016), cotton (Xie et al., 2015), and *M. truncatula* (Wang et al., 2011) where miR398 was found to regulate the expression of *CSD1* and *CSD2* negatively. Along with the SODs, miR396 was also predicted to regulate the expression of glutathione peroxidase genes (*BnGPX13* and *BnGPX20) in Brassica napus* under drought stress conditions (J. Li et al., 2022). It is highly likely that miRNAs are involved in the regulation of other antioxidant enzymes, however, those links are yet to be explored. These identified miRNAs and their involvement in mitigating the adverse effects of oxidative stress point out the possibility to exploit the benefits of miRNAs to introduce drought-resilient crops. The identification of novel miRNAs from the genome of various plants, especially drought-tolerant plants, is essential to further improve our present understanding of the mechanism of miRNAs mediated ROS regulation.

6. miRNA-mediated regulation of metabolism under drought stress

Plants that grow in natural environments encounter various stresses and to withstand such adverse conditions, they initiate a complex signaling which allows plants to adapt to stress conditions (Jogawat et al., 2021). These adaptive features include changes in primary and secondary metabolism, leading to an accumulation of various primary and secondary metabolites such as osmolytes. Interestingly, a growing body of evidence indicates an active role of miRNAs in the regulation of primary as well as secondary metabolism under drought stress conditions. For instance, Selvi et al. (2021), identified differentially expressed *MIR* genes and their targets related to the carbohydrate transport and metabolism under drought stress in sugarcane. The target genes of tae-miR5384-3p, sbi-miR397-3p, and hvu-miR444b which were all downregulated under drought stress included glyceraldehyde 3-phosphate dehydrogenase, invertases, and alpha-galactosidase respectively, that are involved in carbohydrate transport and metabolism (Selvi et al., 2021). In addition, a downregulation of miR397, which targets a β-fructofuranosidase enzyme, associated with starch and sucrose metabolism was observed in drought-tolerant rice variety having higher sucrose metabolism whereas the opposite results were observed in a drought-susceptible variety (Cheah et al., 2015). These results indicate that miRNAs that induce the silencing of genes associated with carbohydrate metabolism and transport are downregulated which favors higher carbohydrate metabolism required for drought stress tolerance.

In the case of secondary metabolism, a miR172c was identified that negatively regulates the lignin biosynthesis in plants. Lignin deposition over the cell wall provides mechanical strength and is a crucial adaptive feature to withstand drought stress conditions. miR172c-5p targets the *ferulate 5 hydroxylase (F5H)* gene responsible for lignin biosynthesis during drought stress and overexpression of its precursor resulted in reduced lignification and secondary xylem thickness in *Bacopa monnieri* (Jeena et al., 2021). In addition to the *F5H*, a recent GWAS study in *Phyllostachys edulis* identified putative miR397 binding sites in the coding region of laccase gene *PeLAC10,* which also play a key role in the lignin biosynthesis (Li et al., 2020). Heterologous expression of *PeLAC10* in Arabidopsis resulted in lower levels of malondialdehyde and higher levels of lignin that enhanced the drought tolerance of the transgenic lines as compared to the wild type (Li et al., 2020). In Arabidopsis, miR858 is involved in the silencing of MYB transcription factors including MYB11, MYB12, and MYB111 that regulate flavonols biosynthesis. Heterologous expression of Arabidopsis *miR858* in tobacco led to drought stress sensitivity via the negative regulation of the flavonoid biosynthesis by decreasing the expression of *NtMYB12* and other associated genes of the phenylpropanoid pathway (Sharma et al., 2022). Likewise, in rice, MIR171f is not only involved in the developmental process but also regulates the drought stress response via upregulating the genes associated with the biosynthesis of flavonoids such as *OsCHS*, *OsCHI*, *OsF3H*, *OsF3′H*, *OsFNSII*, *Os4CL2*, and *OsF2H*. During drought stress, MIR171f majorly downregulates the transcript level of *SCARECROW-LIKE6-1 (SCL6-I)* and (*SCL6-II)* which are the negative regulators of flavonoid biosynthetic pathway (Um et al., 2022).

These results altogether indicate that miRNAs are involved in the regulation of various primary as well as secondary metabolites including carbohydrates, lignin, and flavonoids that are required for drought stress alleviation.

7. Phytohormones – miRNAs interaction is involved in the fine-tuning of drought stress response

Phytohormones are not only involved in normal plant growth and development but are also vital during challenging environmental conditions. The mechanism associated with drought stress sensing and activation of stress signaling is complex and involves silencing and activation of a plethora of known and yet unknown genes. Roots sense drought stress first and the signal is then transferred to the aerial parts. The ABA-mediated closure of stomata to prevent water loss from aerial parts is one of the earliest events in drought stress response in plants. In addition to ABA, other phytohormones including ethylene, auxin, cytokinin, jasmonic acid, gibberellic acid, brassinosteroids, and strigolactones have also been identified as key components of drought stress responses in plants that regulate other drought stress-induced responses including synthesis of secondary metabolites, modifications of the cell wall, cuticle thickening, and alterations in morphology and anatomy of leaf and root to lower the water loss and oxidative stress (Jogawat et al., 2021). These drought stress responses are categorized into ABA-dependent and/or ABA-independent pathways depending upon the specific requirement of ABA and emerging evidence suggests a key role of various miRNAs in the regulation of both of these drought stress responses in plants.

7.1. ABA-mediated regulation of drought stress

Drought stress triggers the synthesis of ABA in plants which promotes root growth to maximize the water uptake from the soil (Saab et al., 1990). In addition, ABA is also involved in the closure of stomata, improvement of water use efficiency, regulation of hydraulic conductance in roots, and induction of suberization of Casparian strips in root endodermis to increase the plant fitness under drought stress conditions (Ikegami et al., 2009; Kuromori et al., 2018; Manzi et al., 2015). In response to drought stress, alteration in the level of transcription factors including ABA-responsive element binding proteins (AREBs), ABA-binding factors (ABFs), NACs, MYBs, NF–Y, HD-ZIP, and WRKY leads to the regulation of several genes to promote drought stress tolerance (Jan et al., 2019; Khan et al., 2018; Samad et al., 2017). Interestingly, many of these transcription factors such as NF–Y, NAC, and HD-ZIP class of transcription factors are regulated by miRNAs (Sunkar et al., 2012). For instance, a miR164 was identified in rice that regulates the expression levels of *OsNAC* by targeting its mRNA which in turn directly regulates the expression of *OsLEA3* to improve drought tolerance. In addition, the NAC transcription factor also interacts with the *OsNCED3* promoter, a key enzyme of the ABA biosynthetic process, to regulate ABA biosynthesis. Overexpression of *OsNAC2* in rice showed higher drought tolerance with survival rates improved from 11.2% in wild-type to 70% in the overexpression lines. Moreover, the overexpression lines also showed elevated endogenous ABA levels, suggesting a key role of miR164 in regulating the expression of NAC, biosynthesis of ABA, and drought stress response Jiang et al. (2019);

Yang et al., 2019a,b observed that miR165/166 is involved in the regulation of drought stress tolerance via ABA signaling by the regulation of HD-ZIP IIIs transcription factor (Yang et al., 2019a,b). DWD (DDB1 binding WD40) is a negative regulator of ABA signaling and its expression is regulated by miR1876. Under drought stress conditions, the upregulation of miR1876 leads to the downregulation of DWD which in turn inhibits its negative effects on ABA signaling in roots and helps in elevating drought tolerance in rice (Nadarajah and Kumar, 2019). Another miRNA, miR162, is known to be ABA-responsive and was found to be upregulated in Arabidopsis, barley, and maize, but was downregulated in cotton under drought stress (Nadarajah and Kumar, 2019). The detailed mechanism of miR162 function was studied in rice where it was found to target *OsTRE1* (trehalase 1) gene under drought and in response to ABA treatment. The upregulation of miR162 resulted in decreased expression of *OsTRE1* which in turn resulted in lower trehalose accumulation and drought sensitivity. In apple, the Serrate gene (*MdSE*) is known to be a negative regulator of drought tolerance and is involved in the degradation of *MdMYB88* and *MdMYB124* which are the positive regulators of drought stress tolerance (Xuewei Li et al., 2020). *MdMYB88* and *MdMYB124* are involved in the regulation of ABA biosynthesis by regulating the expression of the ABA biosynthesis gene, *MdNCED3*. In addition, MdSE is also involved in the biosynthesis of miR399, a negative regulator of drought stress tolerance, and downregulation of various miRNAs including mdm-miR156, mdm-miR166, mdm-miR172, mdm-miR319, and mdm-miR399 that play a positive role in drought tolerance (Xuewei Li et al., 2020). In rice, ABA biosynthesis was found to be negatively regulated by osa-miR2105 (Gao et al., 2022). Downregulation of the miR2105 through knockout or knockdown showed drought stress tolerance via higher ABA biosynthesis that in turn reduced water loss and improved stomatal closure (Gao et al., 2022). miR2105 is known to target the OsbZIP86 transcription factor which induces the biosynthesis of ABA during drought stress conditions by binding to the promoter sequence of ABA-biosynthesis gene 9-cis-epoxycarotenoid dioxygenase (*OsNCED3*). *OsbZIP86* rice lines also exhibited similar drought tolerance as osa-miR2105 knock-out lines, further indicating an interaction between OsbZIP86 and miR2105 and their effects on the regulation of drought stress tolerance in plants (Gao et al., 2022).

7.2. ABA independent regulation of drought stress

ABA-independent drought stress responses are governed by other phytohormones including ethylene, auxin, salicylic acid, brassinosteroids, jasmonic acids, and gibberellins (Ku et al., 2018; Verma et al., 2016).

7.2.1. Auxin

An important phytohormone, auxin governs several key physiological and developmental processes and acts as a signaling molecule in plants to sense and respond according to the changes in the external environment (Singh et al., 2019). Alterations in the miRNAs have been reported which control the auxin signaling pathway required for growth and development under drought-stress conditions (Ding et al., 2013). For instance, miR390 regulates the production of TAS3-derived trans--acting small interfering RNA (tasi RNA) which controls the development of the lateral roots and maintains the organ polarity through binding of the ARF2, ARF3, and ARF4 transcription factors of the auxin signaling pathway in *Arabidopsis thaliana* (Meng et al., 2010). Likewise, miR160 and miR167 are also involved in the inhibition of the expression of their target ARF10, 16, 17, and ARF6, 8 respectively, thus regulating root growth and development via regulating the auxin levels (Singh et al., 2020a). Recently, Ahmad and co-workers reported that slymiR160, slymiR2199, and slymiR6426 bind to the ARF transcription factors and improve drought stress alleviation via growth retardation to evade the stress condition (Ahmad et al., 2022). In rice, a miR393 was identified which negatively regulates the expression of auxin receptors, *Oryza sativa* transport inhibitor response 1 (OsTIR1) and *Oryza sativa* auxin signaling f-box (OsAFB2). Overexpression of miR393 in rice showed early flowering, increased number of tillers, and tolerance to drought and salinity in transgenic plants, demonstrating the interaction between auxin and miRNA in stress response (Bian et al., 2012). Furthermore, miR167a contributes to the maintenance of proper root architecture of plants under drought stress conditions by lowering the transcript amount of IAA-ALA RESISTANT 3 (IAR3) protein that inhibits the release of bioactive IAA in the Arabidopsis roots (Salvi et al., 2021).

7.2.2. Ethylene

The gaseous hormone ethylene shows dynamic effects on plant growth and development and is a master regulator of ROS homeostasis under stress conditions (Riyazuddin et al., 2020). Emerging evidence suggests that miRNAs regulate the ethylene-mediated stress responses, for instance, drought stress-responsive miR169g was found to be regulated by Ethylene Response Factor (ERFs) (Zhao et al., 2007). Another miRNA, miR164, was found to be negatively affected by the ethylene signaling component EIN2. As plants age, the level of miR164 decreases due to an increase in EIN2, which leads to leaf senescence. However, transgenic Arabidopsis plants overexpressing miR164 exhibited a longer leaf lifespan, possibly because of a change in ethylene signaling through EIN2 (Kim et al., 2009). Elevated ethylene concentration during drought stress promotes leaf senescence which demonstrates yet another connection between the aforementioned mechanism and drought adaptation (Ferdous et al., 2015). Another miRNA, miR528, is one of the most prominently expressed monocot-specific miRNAs which potentially regulate the breakdown of ethylene by acting as a potential target of the XBAT32 E3 ligase, which is known to regulate lateral root growth via its involvement in ethylene biosynthesis (Bertolini et al., 2013; Prasad et al., 2010). The leaves of *Xbat32* mutant plants experienced ethylene-mediated cell cycle arrest due to ethylene overproduction in comparison to the wild type under drought stress. Thus, the control of XBAT32 by miR528 may help to tailor the ethylene-mediated growth responses under drought stress conditions (Bertolini et al., 2013).

7.2.3. GA and BR

Gibberellin acid (GA) is another growth-regulating phytohormone that is well known for its vital role in the floral transition, photomorphogenesis, male fertility, fruit set, leaf, and stem growth, and promoting plant growth via cell division (Hernández-García et al., 2021). In potato, three miR171 family members (miR171a, miR171b, and miR171c) steadily increased during drought stress which activated the expression of the (*Sperm-Coating Protein, SCP*) gene to synthesize the SCL (Scarecrow-like, SCL) protein. The production of SCL has the potential to modify plant root structure and ultimately improve drought tolerance (Liang et al., 2020).

The brassinosteroid (BR)-related gene *OsLAC*, which is connected to grain yield during osmotic stress, is inhibited by the upregulation of miR397 in *O. sativa* and Arabidopsis (Ahmad et al., 2022). Based on *in silico* analysis, a link between co-expressed miR396, miR397, and phytohormones including BR and auxin was highlighted and it was predicted that their crosstalk help in the regulation of growth, development, and crop yield to minimize drought stress-induced damage (Zhou et al., 2010). A drought-inducible bHLH102bHLH/HLH transcription factor is a member of the BR signaling cascade and is involved in cell elongation in cotton plants (Lu et al., 2018). Recent evidence shows that miRNA399 and miRNA396 target the bHLH transcription factor which potentially reduces the stomatal density and thus lowers the loss of water to induce drought stress tolerance in sorghum (Chakraborty et al., 2020). The up-regulation of miRNA (vun_cand015) in drought-tolerant cowpea plants, which target the bHLH transcription factor during exposure to drought stress, was also reported, indicating its role in abiotic stress tolerance (Barrera-Figueroa et al., 2011).

8. miRNA-based approaches for breeding to produce drought stress tolerant crops

A lack of water has a detrimental effect on plant growth and severely limits their productivity (Shakeel et al., 2011). The development and release of drought-tolerant crop varieties are required to meet the food demand for an exponentially growing population under the prevailing drought stress conditions. Recent evidence indicates a pivotal role of miRNAs in the supra-regulation of drought stress response in plants and thus these are the promising candidates that can be targeted to improve the fitness of plants under drought stress. The levels of these miRNAs can be modulated by classical breeding or transgenic approach to develop the plants with the desired phenotype. For instance, transgenic potato plants expressing miRNA which targets two proline dehydrogenase genes (*StProDH1* and *StProDH2*) showed elevated proline content and therefore improved drought stress tolerance (Li et al., 2020).

miRNA397a was identified as a regulator of the biosynthesis of lignin and antioxidants in barley. It was observed that the levels of miRNA397a were decreased in the drought-tolerant genotype whereas it was increased in the drought-sensitive genotype, indicating a negative role of hvu-miR397a in drought stress tolerance (Qiu et al., 2020). Therefore, efforts can be made in the future to suppress the expression of this miRNA to induce drought stress tolerance in susceptible crops. Likewise, miR156-SPL and miR160-ARF modules were recognized as having the ability to suppress metabolism under drought stress in drought-sensitive maize plants (Liu et al., 2019). Further, a total of 16 upregulated and 17 downregulated conserved miRNAs were identified in wild rice plants under drought stress along with their putative target genes which can be screened further to select the right candidate to be targeted for the development of drought stress-tolerant rice cultivars (Zhang, 2015). Conventional breeding and marker-assisted selection techniques have also been employed recently to develop drought resistance crops (Waititu et al., 2020).

8.1. CRISPR/Cas9 approach to target miRNAs for developing drought-resilient crops

With the recent advancement in biotechnological tools, targeted genome editing is becoming easier to develop transgenic crops that are better suited for adverse environmental conditions with improved yields. One of the revolutionizing techniques of genome editing is Clustered Regularly Interspaced Short Palindromic Repeats (CRISPR/Cas9) which is utilized widely to create transgenic plants more efficiently than any other available molecular techniques. It cleaves the genomic DNA by a short non-coding RNA, leading to gene modification via non-homologous end joining and homology-directed repair processes (Rani et al., 2016). CRISPR-Cas9 technology has been preferred to create miRNA knockout mutants over other technologies as it is more efficient, cost-effective, precise, and rapid at editing the genome (Haque et al., 2018). Although there are limited data available related to the application of CRISPR/Cas9 technology in the miRNAs-mediated drought stress tolerance in crops, emerging evidence supports a key role of this technology in developing drought-resilient plants in the future. For instance, a miR168, which is known to be downregulated under drought stress conditions in Arabidopsis (Liu et al., 2008) and tobacco (Chen et al., 2017), was knocked-down by CRISPR-Cas9 in rice. In the T1 generation of rice, destruction of pre-miR168a stem-loop structure was observed, which increased the number of tillers, and promoted early maturation of tillers and seedlings, elucidating the role of miR168a in the regulation of agronomically important traits along with drought stress tolerance (Zhou et al., 2022). Another study on rice also utilized CRISPR-Cas9 to disrupt the stem-loop structure of OsmiR535, which enhanced the survival rate of the mutant rice plants by 30% as compared to wild-type under PEG-induced drought stress (Yue et al., 2020). Likewise, CRISPR-Cas9 was also utilized to target the drought-responsive miRNAs, miR396 and miR172 (Bakhshi et al., 2016; Zhou et al., 2010), however, those studies did not investigate the effects of drought stress on mutant lines. As the expressions of these miRNAs are altered in response to drought stress, it would be interesting to analyze the effect of drought stress on these mutant lines in the future (Zhang et al., 2020).

8.2. Short tandem target mimic (STTM)

Short Tandem Target Mimic (STTM) is a technology developed to inhibit the inhibitory function of miRNAs on mRNA expression. STTM binds to complementary miRNAs and disrupts their functions leading to the normal expression of the target mRNAs (Yan et al., 2012). For example, mutations were induced in miR165/166 and miR160 that play a vital role in leaf development and drought stress tolerance via artificially designed nucleotide STTM. The double mutants (STTM160 × STTM165/166) Arabidopsis plants showed compromised leaf phenotype but enhanced drought tolerance in comparison to wild types and single mutants (Yang et al., 2019a). Likewise, the knockdown of miR166 in rice plants by STTM technique showed higher drought tolerance along with smaller bulliform cells and abnormal sclerenchyma cells with a reduced diameter of the stem xylem vessels (Zhang et al., 2018). Moreover, transgenic STTM172 lines targeting miR172 in rice plants showed defects in the main stem and panicle development in comparison to wild types under drought stress (Zhang et al., 2017).

Taken together, available literature identifies putative miRNAs and their target genes under drought stress which can further be utilized to make transgenic plants with better adaptability to changing climate and water scarcity.

9. Conclusions and future perspectives

Drought stress is the most prevailing abiotic stress around the globe and the affected agricultural land is predicted to be further increased in the upcoming decades. Therefore, drought-tolerant crops need to be developed to ensure food for the rapidly expanding population in the coming years. Emerging evidence suggests that miRNAs have huge potential in improving plant performance under drought-stress conditions. miRNAs showed a regulatory role in the detoxification of drought-induced ROS by regulating the expression of various genes encoding for enzymatic and non-enzymatic antioxidants. Besides, miRNAs also regulate phytohormone signaling and modulate drought-responsive genes to enhance plant drought stress tolerance.

Although miRNAs-based approaches have been utilized to produce drought-tolerant crops, more research work is still required to completely understand the complex mechanisms of miRNAs-based drought tolerance. For instance, efforts can be made to identify yet unknown lncRNAs, miRNAs, their downstream targets, and their effects on drought stress resilience in different plants using available molecular biology tools. Moreover, attempts can also be made to identify new miRNAs and their putative targets via *in silico* approaches to hypothesize their roles in drought stress. Besides, it is also crucial to characterize the cis-regulatory elements of *MIR* genes, and the signaling pathways critical for miRNA regulation prior to attempting the miRNAs-based development of drought stress tolerant crops to minimize the undesired negative effects. Additionally, more studies need to be focused on the characterization of the cis-regulatory elements of various miRNAs governed by drought stress to find the reciprocal transcription factors involved in plant growth, and development under drought stress conditions. Furthermore, it is also crucial to know their roles in the epigenetic regulation of several traits such as regeneration of plant tissue, the transition of vegetative phase or vice versa, and rejuvenation under drought stress conditions that will help to understand the possible molecular mechanisms of epigenetic memory and can be utilized by plant breeders to develop the drought-resilient crops.

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Authors' contributions

Conceptualization, R.G., K.S., and R.R.; writing—original draft preparation, R.R., K.S., N.I., M.U.; writing—review and editing, R.G.; V. P.S., N.L., and P.W.R., read the manuscript and add critical values, R.G.; supervision, R.G. All authors have read and agreed to the published version of the manuscript.

Declaration of competing interest

The authors declare that they have no conflict of interest.

Data availability

No data was used for the research described in the article.

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