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MicroRNAs: A big player to mitigation towards abiotic stress in economically importance plants under climate change conditions

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Abstract: MicroRNAs are 20-24nt long, endogenous, and non-coding RNAs that play key role in the regulation of gene expression during the growth and development of plants. miRNAs act as a negative regulator of their target genes by sequence-specific cleavage of mRNA, chromatin modifications or translational repression for stress tolerance. Recently, "food security" has become the biggest challenge of our world due to the abiotic stress that affected the plant growth and productivity. Abiotic stress is induced at the cellular and molecular level in plants. Studies have shown that miRNA and genotype dependencies exist in the response of miRNAs to abiotic stimuli in tissue. miRNAs regulate the genes by TFs within the network of miRNA target genes, and the signalling pathways under abiotic stress. Nowadays, the majority of research focused on the recognition of miRNAs that are responsive to numerous stress conditions and examined their expression profile that modify during these treatments. In the future, more studies on gene expression and function will be required to elucidate the common miRNA-mediated regulatory mechanisms that enhances abiotic stress tolerance. The communication involved in regulating abiotic stress response by the up and down regulation of target TF and functional proteins are highlighted in this review.

Keywords: MiRNA; Abiotic stress; Gene expression; RNA polymerase II; Dicer

1. Introduction

The global climate change, alter the environmental conditions and soils, which can cause problem in plant growth and development (Zhang et al., 2018). It is called "environmental abiotic stresses" due to drought, cold and salinity, significantly affect plant growth, survival and development, and thus decrease plant yield, quality, and biomass production (Zhang et al., 2022; Liang et al., 2010; Mittler, 2006). Abiotic stress effects may also reflect at various sub organismal levels, including at the physiological, cellular, biochemical, organismal, and finally at the morpho-physiological level. Several studies have exhibited that abiotic stress reduce seedling development and germination, chlorophyll biosynthesis, photosynthesis and root development and that damage plant growth and development, further prompted oxidative stresses (Suzuki et al., 2014; Liang et al., 2010; Mittler, 2006). The abiotic stresses have also been exhibited to change gene expression profiles significantly during various developmental phases; these gene expression programmes change and finally regulate plant growth, development and plasticity timing (Mathur et al., 2014). Numerous important genes, involving those encoding TF, have been implicated in abiotic stress response and when these genes were upregulated in model plant species, for instance A. thaliana, as well as other agriculturally essential crops, they were exhibited to plant tolerance improvement for particular stresses significantly (Tamirisa et al., 2014).

MicroRNA (miRNA) are 20-24 nucleotide long, non-coding RNA and about that involved in transcriptional and post-transcriptional gene regulation. These miRNAs regulate gene expression by either cutting the target mRNA or repressing translation (Biswas et al., 2021; Wu, 2013).

A prosperity of various miRNAs has been explained by computer algorithm prediction, small RNA cloning, and big throughput sequencing in both eukaryotes and prokaryotes, lots of that showed to lay crucial roles in plant growth and development. The first miRNA was recognized in the worm Caenorhabditis elegans by Ambross and colleagues in 1993. The principal members of miRNAs were let-7 and lin-4 that initially recognized as a key regulator of the juvenile-adult larval development in C. elegans. miRNA of heterochronic, encoded by lin-7 interacts with targets and suppress the expression. In plants, the first miRNA was discovered in Arabidopsis thaliana. There are thousands of miRNAs have now been stated in dozens of plants and animals. Plants, in which miRNAs have been identified are Arabidopsis, Populus, Physcomitrella, Sorghum, rice, maize, sugarcane, soybean etc.

The genome of plant typically encoded a hundred of genes of miRNA, in which most of them present as a family member (Budak & Akpinar, 2015). On the basis of their position in the plant genome the miRNAs are categorized as an "intergenic" or "intronic". The intergenic miRNAs are transcribed via DNA-dependent RNA polymerase II and are situated between 2 protein encoding genes, whereas, intronic miRNAs are treated from introns of their host transcripts (Wang et al., 2019). It enrolled by the mediator to promoters (coactivators) of miRNAs to form 5′ capped, spliced and 3′ polyadenylated-tail primary miRNAs (pri-miRNAs) (Kim et al., 2011). Pri-miRNAs are processed in a hairpin loop like formation comprising of an upper stem, two arms, a lower stem, a terminal loop, and the miRNA/miRNA* region, which can be identified and processed by a combined action of Dicer-like (DCLs RNase III endonucleases) protein (Wu, 2013). miRNA's productions are catalysed by DCL1 with the help of accessory proteins consisting with dsRNA binding (DRB) protein, HYL1 and C2H2-like zinc-finger protein (SE) SERRATE. Other DCL protein may also be engaged in the formation of miRNA (Sunkar et al., 2012). The duplex of miRNA/miRNA* produced by DCL shows protein-mediated processing, the 1 nt - 35 nt overhangs at both strands and acquires two 3′ end -OH and a 5′ end phosphate. Whereas both -OH are crucial, only the 2′-OH site is methylated through the HEN1 i.e., a small RNA methyltransferase (Budak & Akpinar, 2015; Yang et al., 2006). The former methylated duplexes are considered to be transferred through the exportin 5 (EXPO5) homologous proteins HASTY (HST) shows in fig 1 (Wu, 2013).

Currently, a study exhibited that the primary assemblage of RISC complex is in the nucleus and after that transferred to cytosol through EXPO1 (Bologna et al., 2018; Bechtold & Field, 2018). Accordingly, current available data confirm the possibility that several miRNAs are exported in duplex pattern and assemble in cytoplasm. The passenger strand i.e., miRNA* was degraded and the guide strand of miRNA duplex was assembled selectively into the AGO (Argonaute) protein. A. thaliana has ten AGO proteins, comprising AGO1 present as a main effector protein for miRNAs (Wu, 2013). The miRNAs lead the RISC protein to target genes via base pairing and mostly facilitate gene silencing through translation inhibition and target cleavage. However, latest reports also show the role of RISC/AGO1 in transcriptional regulation (Yang et al., 2019; Enebe & Babalola, 2018). Few miRNAs such as miR845, miR173 and miR390 are capable of starting the formation of secondary siRNAs (Daugaard Hansen, 2017). In plants, identification of miRNAs based on cloning or genetic engineering and sequencing of small RNA libraries in which experimental approach and computational prediction method of conserved miRNAs are present. The miRNAs regulate the gene expression at different steps of development and growth in plants (Djami-Tchatchou et al., 2017). There are several roles of miRNAs in plant developmental process, biotic and abiotic stress, nutritional deficiency, and pathogen infection (Zhang, 2015). RNAi mediated miRNA used to change the gene expression of crop plants without adding new proteins to find better crop traits with better quality like enhanced nutritive value, reduced toxin, abiotic, and biotic stress tolerance etc. (Brant & Budak, 2018).

2. Roles of miRNAs in plant growth and regulation

The miRNAs are crucial regulators of the plant responses to the abiotic stress (fig 2). miRNA also holds the capability to show genotype and species-specific expression patterns during abiotic stress conditions. In plants, gene mutations are involved in the biogenesis and the miRNAs regulatory roles show the strong effects on the development (Xie et al., 2010). The essential

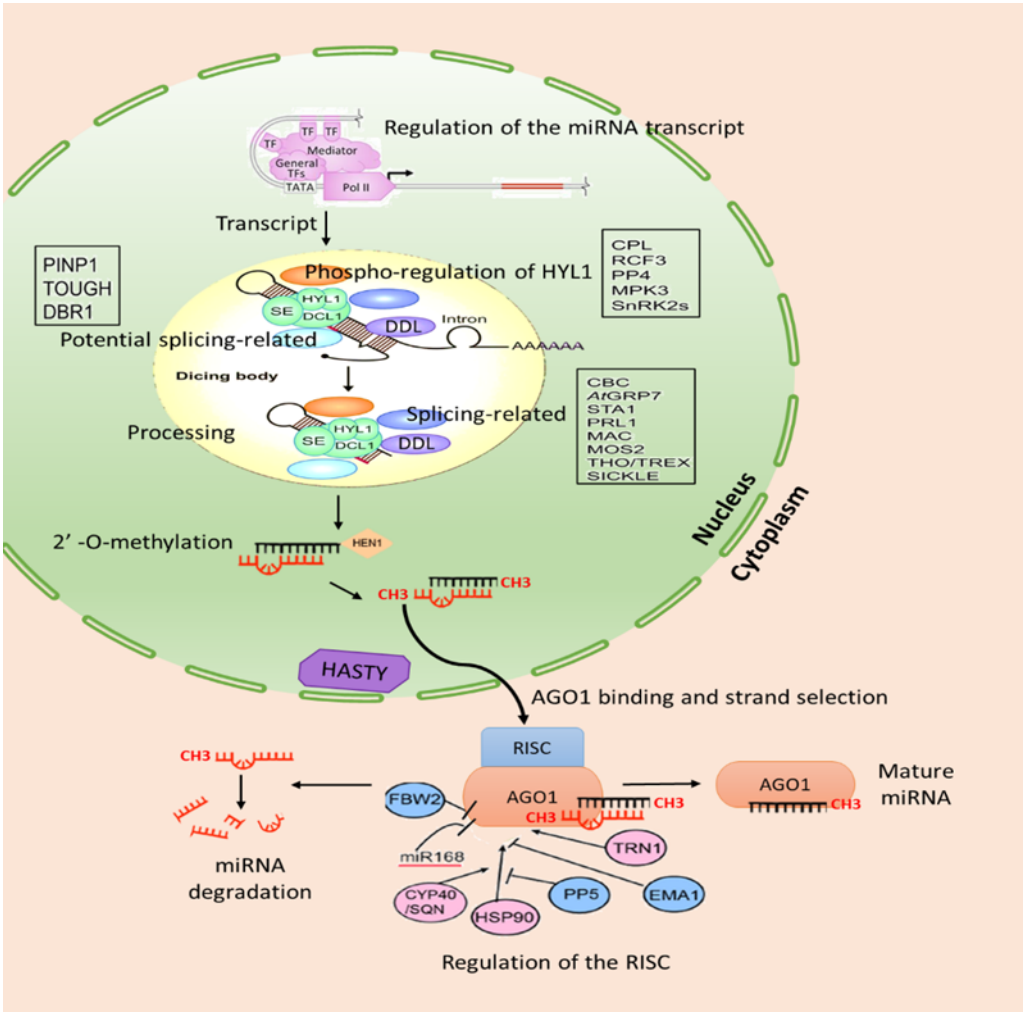

Figure 1. Regulation of microRNA biogenesis and its mechanism of action is illustrated in the figure. Firstly, the RNA Pol II is transcribed by miRNA genes, the former is converted intopri-miRNAs which has a stem-loop like structure. Secondly the pri-miRNAs are processed by DCL1 followed by methylation of miRNA duplexes by HEN1 i.e., small RNA methyltransferase. Lastly, the loading of the RISC complex occurs in the cytoplasm and ultimate miRNA mediated silencing either by translation inhibition or target cleavage (For further detail see text) cleavage of target mRNA, (2) translational repression, and (3) transcriptional silencing.

role of miRNAs in plant growth and development is exhibited by these effects (Liam et al., 2012). The AGO genes, mainly miR168a and miR168b regulated AGO1, which play an important role in the stabilization and the regulatory role of other miRNAs (Sieber et al., 2007). In A. thaliana plant, under standard growth conditions the overlapping functions between different miR168 family members, and mutations or alteration in the miR168a gene did not alter the plant development process (Vaucheret et al., 2004). In A. thaliana, the TFs coding genes cup-shaped cotyledon (CUC) and NO APICAL MERISTEM (NAM-NAC) are regulated via the miR164 family, that are essential in shoot and root development. In floral development, the miR164abc triple mutants showed, the genes athMIR164b and athMIR164a overlap the function of athMIR164c partially, as the

phenotype became more acute in the triple mutant (Sieber et al., 2007). For the proper root development, the scarecrow like (SCR) and short root (SHR) proteins trigger the miR166b and miR165a genes, which in turn adversely control the HD-ZipIII TF (Carlsbecker et al., 2010).

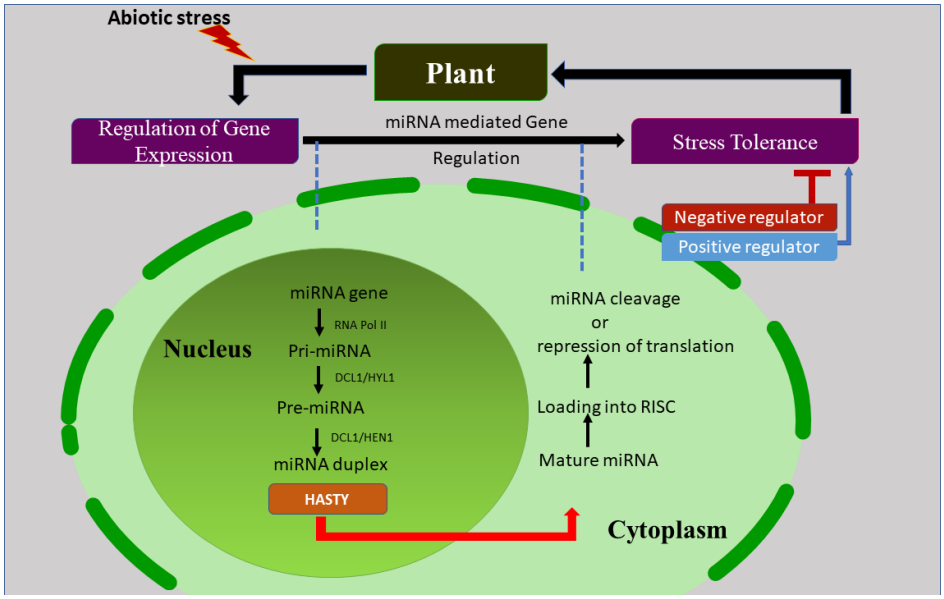

Figure 2. Schematic representation of miRNA mediated regulatory responses in the plant during abiotic stress condition. The diagram represents the process of miRNAs formation from miRNA genes and miRNA mediated gene regulation in plants under abiotic stress. During stress, miRNA genes are initially transcribed via RNA Pol II to apri-miRNA, which further processed into a pre-miRNA. With the help of DCL1 (dicer like enzyme), a miRNA:miRNA* duplex miRNA is formed from the hairpin and then the miRNA:miRNA* duplex transported from nucleus to cytoplasm through the enzyme HST. The mature miRNA is combined into the RISC (RNA-induced silencing complex) which guides the miRNA to regulate the targeted gene expression by mRNA cleavage or translational repression. Thus, finally the miRNA mediated positive or negative regulation of target genes confers to stress tolerance in plant.

In the plant development, miR156 play an important role which controlling the phase transition. The known function of miR156, regulates the SPL genes and those plants inducing miR156 showed longer vegetative phase, altered number of leaves and semi-dwarf. The suppression of miR156 gene from the young to the mature phase is in comparison to the over expression of miR172, which is the significant regulator of the floral pattern formation genes for instances TOE1/2 and APETALA2 (Liu et al., 2018). Interestingly, the principal mutant corngrass (Cg1), that contains 2 tandem miR156 genes, exhibited an up regulation of miR156 in the lateral organs and meristem, and diminishes miR172 levels. These mutants aided in identification of the regulatory functions for these conserved miRNAs in the progression from young to the reproductive phases in crop plants like rice and maize (corn) (Yang et al., 2011). The leaf primordia ablation, hindered the reproductive phase transition, exposing that transcriptional signal that modulates miR156 regulatory action were obtained to be necessary to shift in plant phases (Yang et al., 2011).

In the maize crop, the spatial expression of miR156 regulates the TF ZmTSH4, is essential for the lateral meristem formation (Song et al., 2011; Chuck et al., 2010). Using different approaches such as sequencing and degradome around 26 new miRNAs and their respective gene of interest was recognized throughout the various developmental stages of seeds in soybean (Liu et

al., 2018). The hormone signalling and gene expression during miRNA regulation also have an important role in plant development. In A. thaliana, miR159 targeting members of the GAMYB (gibberellic acid MYB) family regulates anther formation and seed germination (Reyes & Chua, 2007), whereas downstream genes like GAMYB suppress the floral transition. The miR159 is a crucial miRNA that has the capability to regulate the development of male reproductive organs by affecting MYB family genes. In A. thaliana and rice plant, miR159 is over-expressed in the anthers and its up-regulation causes male sterility subsequent from the failure of pollen release and delayed flowering (Liu et al., 2018; Miller & Gubler, 2005). Biosynthesis of jasmonic acid (JA) are regulated through TCP TFs which have functional roles in leaf senescence and development and are controlled through miR319 (Liu et al., 2007). In the auxin signalling pathway, miRNA also targets functional genes with auxin response factors (ARFs). In plants, miR160-resistant forms of the ARF 10, 16 and 17 genes that exhibited pleiotropic effects in roots and shoots (Liu et al., 2007). The overexpression of miR160 outcomes has inhibited root length, and an enhanced number of lateral roots. During gynoecium and stamen development in a flower the miR167 has a crucial role of targeting genes viz. ARF8 and ARF6 (Liu et al., 2018). In A. thaliana, cell proliferation is reduced through the overexpression of miR396, which repress the genes of growth regulating factor that are important regulators of the cell cycle (Kutter et al., 2007). In Brassicaceae family, the flowering is regulated by miR824 via targeting Agamous like16 gene (AGL16) which shows a species-specific role of miR824-AGL16 in floral transition (Rodriguez et al., 2010).

3. MiRNAs a new target for developing to abiotic stress tolerance

miRNAs have been recognized as a major regulator in plant growth, development as well as a response to several stress conditions shows in fig. 4. Plants are continually challenged by various environmental stresses; they need fast and proper response to survive (Zhang et al., 2018). Several studies have shown that miRNA is situated at the centre of the complex gene regulatory system. Therefore, physiological and morphological adaptations to environmental stresses require complex changes in gene expression network regulated at transcriptional and post-transcriptional level (Zhang, 2015; Barciszewska-Pacak et al., 2015). There are various genes are targeted through miRNAs that encodes transcription factor, this places miRNA is a central hub within the regulation of protein-DNA and protein-protein interactions in plant growth and development. Furthermore, these transcription factors regulate the crucial developmental activities such as phase transition, cell division, organ differentiation and nutrition homeostasis, thus function as an effector of miRNAs in a plant growth and development. That exhibit miRNAs are becoming a new target in various stress tolerance in plants. Numerous miRNAs have been identified as an abiotic stress regulated in chief crops and model plants under salinity, nutrient stress, UV-B radiation, drought and metal stress (Shriram et al., 2016). Several studies have shown that all abiotic stress induce the unusual expression of miRNA in a stress and dose dependent manner. An understanding the molecular process of miRNA action in abiotic stress may provide an effective tool for plant breeding, primarily in the case of anthropogenic and climatic changes in the environment.

3.1. Drought stress

Drought stress is one of the common plant abiotic stress factors, that affect the physiological and morphological structure of plants by affecting the plant growth, development, yield, hormone metabolism, mineral absorption and protein metabolism. miRNA role was shown in the drought stress response that studied in detail in several plants, both upregulation and downregulation were analysed in different miRNAs in response to drought (Sun et al., 2019; Koroban et al., 2016; Sunkar et al., 2012) (fig 3). Due to drought stress, adverse changes occur in the expression of miRNAs that were shown even for one family in some plants; such as, miR319 family miRNAs in rice (Biswas et al., 2021). In M. truncatula, miR398a/b expression was increase/decrease in drought stress accordingly to several reports. microRNA gene expression profiling during drought stress has now been presented in A. thaliana and rice. In A. thaliana, miR319, miR167, miR168, miR159, miR156, miR394, miR171, miR393, miR169 and miR158 were exposed

to be drought responsive. The overexpression of miR393, miR397 and miR319 in response to dehydration in A. thaliana has been stated. In rice plant, miR169g was strongly overexpressed whereas miR393 was transiently stimulated by drought (Khraiwesh et al., 2012).

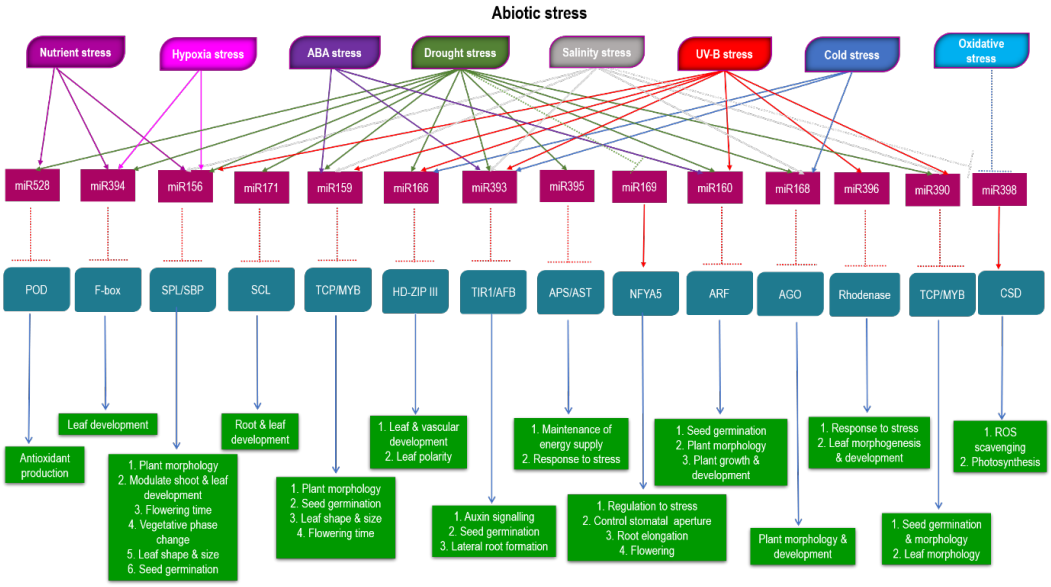

Figure 3. miRNAs regulatory network in plant under abiotic stress. The intended network describes the molecular procedures that lead to phenotypic modifications in plant in response to abiotic stresses. The network is merely based on modifications in miRNA expression patterns and later target transcripts in abiotic stressed plants. A blunt arrow indicates a decrease whereas the arrow represents an enhance in the expression of the corresponding miRNA. POD, peroxidases; F-BOX, SPL sporocyteless /SBP Squamosa promoter Binding Protein; SCL, scarecrow-like 3; TCP, Teosinte branched1 cycloidea PCF /MYB myeloblastosis; HDZIPIII, homeodomain-leucine zipper 3; TIR1 Transport inhibitor response1 /AFB Auxin signalling F-Box; APS ATP sulfurylase /AST Sulfate transporter; NFYA5 Nuclear transcription factor Y Subunit A-5; ARF, auxin response factor; AGO, Argonaute-1; CSD, copper/zinc superoxide dismutase.

In plants, drought stress treatment stimulates the expression of several miRNAs such as miR319, miR156, miR159, miR167 while the expression fold change varies from miRNA to miRNA (Zhang, 2015). Few miRNAs for instance miR169 were downregulated by drought stress treatment. miR169 involved in drought stress resistance via NFY-A5 (target Nuclear Factor YA5) transcription factor in plants. NFY-A5 TF contains a target site for miR169 that targets mRNA for translational repression. The down-regulated miR169 contribute to the enhancement of NFY-A5 expression during drought stress. miR393 and miR169g were observed to be overexpressed during drought stress response in rice plant (Zhang, 2015; Kumar, 2014). The upregulated miR393 targets TIR1 (Transport inhibitor response 1) that triggering a reduction in plant growth and development in drought stress condition. miR160 involved in drought stress related auxin signalling by controlling the expression of ARF (auxin response factor) TFs (ARF10, ARF16 and ARF17), which are involved in plant growth, development and stress response (Sun et al., 2019). miR167 targeting factors response to ARFs (ARF6 and ARF8) whereas miR390 targets ARF4. Under drought stress, down-regulated miRNAs (for instances miR528, miR168 and miR167) may affect the expression of the target genes (POD, PLD and MAPK), thus initiating ABA-inducing regulating of stomatal movement and antioxidant defense. miRNAs such as miR166, miR171, miR408 were also induced by drought stress. miR156 plays an important role in plant

growth, development and phase change. Current- studies exhibited that miR156 was apparently expressed during drought stress (Waititu et al. 2020; Zhang 2015). miR535, miR156 and miR529 target SPLs that regulate plant and differential organ development. Down regulated miR159 enhances the MYB expression and diminishes the plant growth. Additionally, MYB also play a major role PCD (programmed cell death) (Nadarajah &Kumar, 2019; Zhang, 2015).

Under drought stress condition, miR166 play a major role in regulation of lateral root formation and root and leaf morphology in plant. In addition, miR166 through the post-transcriptional regulation of HD-ZIPIII (homeodomain-leucine zipper 3) TF results in cell development of leaves, meristem and roots. However, overexpression of miR166 level, HD-ZIP TF is supressed, resulting in diminishing the lateral root development, xylem diameter and leaf rolling during enhance drought condition. Under drought stress conditions, transgenic Arabidopsis plants, overexpression of miR394 inhibits the H_2O loss during leaf transpiration, which eventually enhanced tolerance to drought stress. miR393 has become a target for improving plant drought stress tolerance (Nadarajah & Kumar, 2019; Sun et al., 2019). Several studies elucidated that overexpression of miR395 alters the plant tolerance to drought stress, as demonstrated by a reduction in seedling growth and seed germination. miR395 participate in plant drought stress resistance via APS (ATP sulphurylase). APS is an enzyme that involved in catalysis of inorganic sulphate assimilation, contains a target site for miR395, which is responsive to the sulphate level in the plant (Sun et al., 2019; Zhang, 2015).

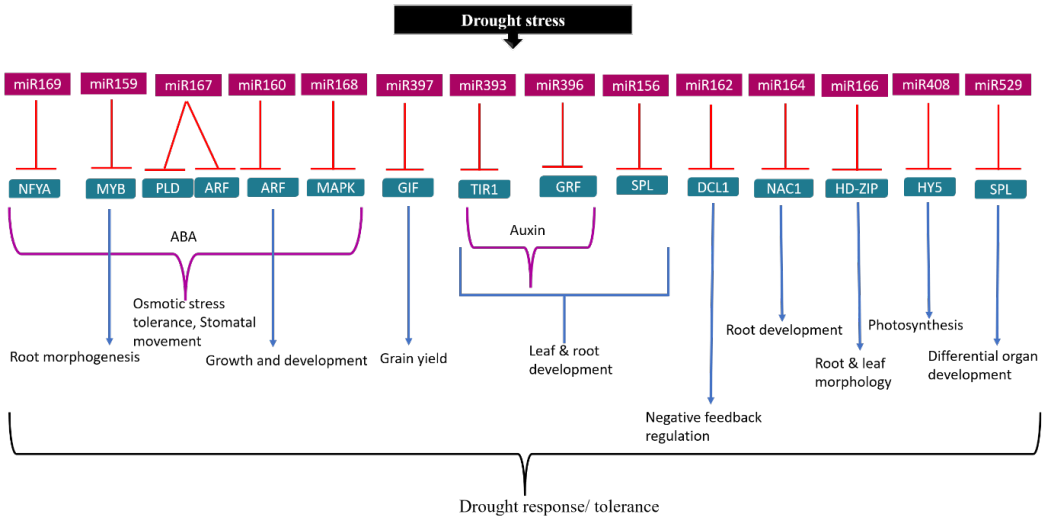

Figure 4. Plant miRNAs have been involved in several abiotic stress responses under drought stress condition. miRNA gene expression profiling shows that miRNAs that are involved in plant growth and development are differentially expressed under abiotic stress responses.

3.2. Salinity stress

Excess soluble salt (salinity stress) in soil negatively affects the quantity and quality of various crop production. Salinity stress is a factor for plants, leading to genome instability, metabolic activity changes, membrane permeability, cytoplasmic lysis and cell wall damage (Afzal et al., 2019; Sun et al., 2019). The plant adaptive response to salinity stress includes alterations in various cellular, molecular processes, for instances signal transduction, photosynthesis, membrane transport, transcription, protein biosynthesis and degradation (Macovei & Tuteja, 2012). The adaptive response to salinity generally develops similar to the drought stress response, proceeding through the involving same transcription factors or same molecular mechanism.

Such as, miR160, miR169, miR167 and miR393 were expressed to play a key role in the salinity response (Koroban et al., 2016). The miR171 and miR396 were expressed differently in the maximum case. In Oryza sativa plant, osa-miR393 upregulated during salt stress, showing their regulatory role in salinity stress tolerance, but also osa-miR393b expression remains same (Lofit et al., 2017). In radish plant, identified 22 novel salt and 49 known stress-responsive miRNAs and target estimation analysis shows the significance of the target genes in the regulation of ion and cellular homeostasis besides signalling, modulating the reduced plant growth in salt stress (Shriram et al., 2016). Under salinity stress induced the expression of miR159, miR319, miR397, miR394 and miR156 in plants, while with varying fold changes. miR398 gene expression was inhibited significantly (Zhang, 2015).

miRNA expression and the target can be induced by salinity stress. When salt stress studying on cotton plants, miR827, miR169, miR535 and miR156 were significantly downregulated, whereas miR397, miR399 and miR167 were upregulated. Additionally, miR156-SPL2, miR162-DCL1, miR395-APS1, miR159-TCP3 and miR396-GRF1 exhibit regulatory relationship in cotton roots and leaves (Sun et al., 2019; Zhang, 2015).

3.3. Nutrient stress

Mineral nutrients are fundamentally important in plants N, Pi and K are three most important plant macronutrients that are generally deficient in soils (Islam et al., 2022; Afzal et al., 2019; Lu & Huang, 2008). Nitrogen is a major component of proteins, amino acid, nucleic acid and coenzymes and it plays an important role in plant growth. miR399 was recognized in rice (Oryza sativa) and Arabidopsis thaliana (Zeng et al., 2014). In A. thaliana, the miR399 target a gene encoding known as ubiquitin-conjugating enzyme (UBC) (Lu and Huang 2008). Fujii et al. (2005) identified, that there is no generous regulation of miR399 by cold, salt, or high temperature stress. Low N or K did not stimulate the expression miR399. But it was observed that miR399 play an important role in the plant response to phosphate (Pi) deficiency by regulating PHO_2 expression, which codes for E2 ubiquitin-conjugating enzyme and is involved in Pi homeostasis (Koroban et al., 2016). The miR399 was strongly induced while the target mRNA UBC was downregulated by (Pi) low phosphate stress. The constitutive miR399 expression in the transgenic plants, UBC mRNA aggregation was repressed even under high concentration of Pi. The accumulation of UBC mRNA, repress by miR399 via targeting 5′ untranslated regions (UTR), and their regulation is significant during Pi deficiency in plants. APS proteins are complementary to miR395 as seen in soil grown plants, whereas, miR395 was not founded in the samples from plants grown in 2mM sulphate (SO_4). But, miR395 was easily found in the samples grown in 0.02-0.2 mM SO_4. The miR395 expression is induced in SO_4 deficiency, whereas downregulated in phosphate, carbon, and nitrogen deficiencies (Koroban et al., 2016). miR398, miR395 and other miRNAs are also involved in plant tolerance enhancement to nutrient stress. Hence, it can be suggested that miRNA has functional roles in plants, they bring variation that helps plants to regulate nutrient accessibility in the soil (Sun et al., 2019).

3.4. Low temperature or cold stress

Low temperature stress affects plant growth by interfering or damaging the cell structure and metabolism. Recent studies have revealed that low temperature or cold acclimation can be regulated at transcriptional or post-transcriptional level (Sun et al., 2019). Important crops for instances rice, cotton, corn and tomato are sensitive to cold and unable to tolerate ice synthesis in their tissues. The miRNAs expression in cold stress has been studied in A. thaliana, Brachypodium and Populus miR397 and miR160 are responding to cold stress in wheat, Arabidopsis and rice. miR169 and miR397 were overexpressed in all 3 species, and miR172 was upregulated in Brachypodium and Arabidopsis (Sun et al., 2019; Thiebaut et al., 2012). In addition to these miRNAs, some miRNAs (miR393, miR408, miR165, miR166 and miR396) were triggered under low temperature stress in A. thaliana, whereas other miRNAs (miR159/319, miR156/157, miR394, miR398 and miR164) showed mild regulation under low temperature stress. In Populus, miR477a,b and miR168a,b were upregulated, whereas, miR156g-j, miR476a and miR475a,b

were downregulated under cold or low temperature stress (Kheaiwesh et al., 2012).

3.5. Oxidative and Hypoxia stress

Stress-induced ROS aggregation is prevented by plant antioxidant systems that comprise of several enzymatic scavengers; SODs (superoxide dismutase) constitute the 1^{st} line of defense against very poisonous superoxide radicals. ROS are inherent to plant due a constant production of ROS through aerobic processes in peroxisome, chloroplasts and mitochondria (Khraiwesh et al., 2012). SODs (superoxide dismutase) help in the ROS scavenging by transforming molecular oxygen (O_2) to hydrogen peroxide (H_2O_2). Metal cofactor that used, SODs (superoxide dismutase) are categorized into 3 groups; Cu/Zn-SOD, Fe-SOD and Mn-SOD (Lu & Huang, 2008). Increased levels of ROS are often connected with plant stress for instances UV radiation, high light intensity, heavy metals, extreme temperature, drought stress, mechanical stress and salt stress (Khraiwesh et al., 2012). The upregulation of SOD proteins and suppression of miR398 has played an important role in A. thaliana plants during oxidative stress (Lime & Margis, 2012). Though, a direct connection between miRNAs and plant abiotic stress responses has arisen with the recognition of miR398, that targets miR395 and miR399, two Zn/ Cu superoxide dismutase (CSD2 and CSD1), and which target the phosphate transporter (PHO1) and the sulphate transporter (AST68), respectively (Sunkar et al., 2012). Additionally, miR398 has been reported to be directly connected with responses to different stress conditions. miR398 is transcriptionally downregulated, which was essential for the posttranscriptional stimulation of targets CSDs (Cu/Zn superoxide dismutase) coding chloroplastic CSD2 and cytosolic CSD1. Downregulated miR398 led to improved oxidative stress tolerance in plants. CSD regulation may function as a general acclimation response to various stress conditions (Zhu et al., 2011; Bartel, 2009). miR395 was also recognized in response to sulphate starvation (Iyer et al., 2012).

Hypoxia (low-oxygen stress) or anaerobic interferes in the mitochondrial respiration. Low-oxygen stress induces huge modifications in the transcriptome and a shift from aerobic to anaerobic respiration. Current researchers proposed that miRNAs are engaged in plant responses to low-oxygen stress. miRNAs play an important role in hypoxia induced regulation in DNA repair. In seedling, that were submerged, various miRNAs were regulated differently; early during submergence, Zm-miR171, Zm-miR166, Zm-miR399, Os-miR396 and Zm-miR167 were induced, but repressed the At-miR395, Os-miR528, Pt-miR474 and Zm-miR159 (Lima & Margis, 2012). miR167 and miR160 are participate in root development (Betti et al., 2020). miR394 as a mobile signal secreted by the surface layer of the cell that converses stem cell competence to distal meristem through downregulating the F-box protein (Knauer et al., 2013).

3.6. Abscísic àcid stress

The phytohormone ABA regulates several major characteristics of plant growth, development and several physiological processes, for instance, synthesis of seed storage lipids and proteins, seed germination and maturation, tolerance induction and pathogen response (Khraiwesh et al., 2012). In germinating A. thaliana seeds, miR159 enhanced accumulation of ABA treated 1-day old seedling. The miR159 aggregation was maximum at 4 to 8 hours after ABA addition (~5fold). Furthermore, when seedling grown on MS medium were exposed for 8 hours to drought treatment, miR159 level was also enhanced. Compatible with the miR159 upregulation repress the transcript level of MYB101 and MYB33 and renders plants hyposensitive to ABA, while transgenic plants upregulating cleavage-resistant forms of MYB101 and MYB33 are oversensitive. Transcriptome analysis has shown that over fifty percent of the genes regulated via ABA are also governed by salinity or drought, while cold regulated transcriptome studies show less overlap with other stresses (Sah et al., 2016).

Several studies in A. thaliana have also stated that upregulation of miR417 and miR160 and repression of miR398 and miR169 in response to ABA (Khraiwesh et al., 2012). In rice plant, miR319 was over-expressed, while miR169 and miR167 were suppressed in ABA-mediated responses. In the Phaseolus vulgaris, miR2118, miR159.2 and miR393 were induced during ABA treatments, while miR1515, miR2119 and miRS1 were moderately overexpress in response

to ABA. In Physcomitrella patens, the DNA methylation dependence in miRNA levels was also revealed an ABA-responsive PpbHLH-miR1026 regulon. Abscisic acid application caused an enhance of miR1026 and reduction of its PpbHLH target RNA (Koroban et al., 2016). Plant stress responses and miRNAs may also be connected via the point that HYPONASTIC LEAVES 1(hyl1) and cap-binding protein 80/ABA Hypersensitive1 (cbp80/abh1) mutant that are cooperating in miRNA biogenesis are hypersensitive to abscisic acid, a modulator of the gene expression of numerous stress-responsive genes.

3.7. UV-B radiation

Recent studies have revealed that UV radiation shows a negative effect on plant growth, yield and development and there are also current reports on exploring UV radiation for increased accumulation of secondary metabolites. In A. thaliana, computational application was used to recognize miRNAs induced through UV-B radiation (Yang et al., 2019). The twenty-one miRNAs related to eleven miRNA families recognized in that analysis, the following was predicted to be overexpressed under UV-B stress; miR159/319, miR167, miR156/157, miR170/171, miR160, miR164, miR169, miR393, miR172, miR401 and miR398. In A. thaliana and P. tremula, some miRNAs families were overexpressed by UV-B radiation in (miR160, miR156, miR167, miR165, miR164, miR166, miR168 and miR398) (Khraiwesh et al., 2012). As well as the down-regulation of miR472, miR169, miR159, miR393, miR390, miR399 and miR395. Remarkably, three families (miR159, miR393 and miR169) that were predicted to be overexpressed in A. thaliana were repressed in P. tremula, proposing that some UV-B radiation stress responses may be species-specific (Yang et al., 2019). The upregulation of miR398 and the miR395, as well as the particular inversion of gene expression of their targets in response to UV-B in P. tremula, advise there are major differences in the stress- induced metabolic adaption compared with A. thaliana (Lima & Margis, 2012).

4. MiRNA approaches for crop plant improvement

Some experimental reports in A. thaliana plant have exhibited that miRNAs are engaged in numerous biological activities where they play an important role in growth and development, metabolism, genome integrity maintenance, hormone homeostasis, hormone signalling pathways and response to different environmental abiotic stresses (Zheng et al., 2019; Lin et al., 2018; Song et al., 2018). miRNAs have been recognized in plants via genetic screening, high throughput sequencing and bioinformatic analysis. The list of the major databases and computational tools are available for miRNA related analysis is shown in Table 1 These computational tools procure effective ways to predict miRNAs and their target genes in plants, algae, animals, human invertebrates and fungi.

In a study, the miR408 function in reproductive development stays unclear, although it is being well known to play essential roles during vegetative development in A. thaliana. Here, they show that transgenic A. thaliana plants upregulating miR408 have changed morphology, including significantly enlarged leaf area, plant height, length of petiole, silique length and flower size, resulting in increased seed yield and biomass. Overexpression and suppression of miRNA were also showing in some cases using transgenic approaches such as; in a tomato plant, over expression of miR169c induced drought tolerance that give diminished stomata opening and reduced transpiration rate (Gautam et al., 2020; Zhang et al., 2018). In rice plant, down regulation of miR156 is involved in the growth and development of reproductive and vegetative organs, whereas over expression of miR7695 was revealed to resistance against fungal pathogen M. oryga. In another study, they review recent progress in comprehension of the miR156 expression regulation and how miR156-SPLs mediated plant stage affects other processes in A. thaliana. Lin et al. (2018) studies the roles of miR160 during high temperature or heat stress, transgenic A. thaliana plants upregulating precursor miR160 and artificial miR160, which imitate an inhibitor of miR160, were formed. The T-DNA insertion mutants of targets miR160 were also used to analyse their tolerance to heat stress. Outcome presented that upregulating miR160 improved seedling survival and seed germination under heat stress. Organ or

Table 1. Several databases and computational tools have been developed in current times to recognize and predict the miRNAs targets.

S. N.	Name	Link	Description	Reference
1.	TAPIR (target prediction for plant microRNAs)	http://bioinformatics.psb.ugent.be/webtools/tapir/	Prediction of target for plant miRNAs	Bonnet et al., 2010
2.	DMD (Dietary MicroRNA Database)	http://sbbi.unl.edu/dmd/	A database constituting dietary miRNA from 15 plants	Chiang et al., 2015
3.	PMRD (plant miRNAs database)	http://bioinformatics.cau.edu.cn/PMRD/	Database containing plant microRNA	Zhang et al., 2010
4.	PNRD (Plant Non-coding RNA Database)	http://structuralbiology.cau.edu.cn/PNRD/index.php	A reorganized version of PMRD	Yi et al., 2015
5.	Semirna (search for plant microRNAs)	http://www.bioinfocabd.upo.es/semirna/	Assists in search for plant miRNAs via target sequences	Muñoz-Mérida et al., 2012
6.	PmiRKB (plant microRNA knowledge base)	http://bis.zju.edu.cn/pmirkb/	A plant miRNA knowledge base	Meng et al., 2010
7.	MTide	http://bis.zju.edu.cn/MTide/	A combined tool for detect the interaction between miRNA and target in plants	Zhang et al., 2015
8.	PlanTE-MIR (database for transposable element related miRNAs in plant genomes	http://bioinfotool.cp.utfpr.edu.br/plantemirdb/	A database for transposable element-related miRNAs in plants	Lorenzetti et al., 2016
9.	C-mii (Computational miRNA identificaion)	http://www.biotec.or.th/isl/c-mii	It is a tool use for plant miRNA and target recognition	Numnark et al., 2012
10.	miRBase	http://www/mirbase.org	Database of available microRNA sequences and annotation	Kozomara and Griffiths-Jones, 2010
11.	miRPlant	http://www.australianprostatecentre.org/research/ software/mirplant	Combined tool for recognition of microRNA of plant via RNA sequencing information	An et al., 2014
12.	WMP (Wheat MicroRNA Portal)	http://wheat.bioinfo.uqam.ca	A database for abiotic stress retorted microRNAs in wheat plant	Remita et al., 2016
13.	miTRATA	http://wasabi.dbi.udel.edu/~apps/ta/	Tool designed for truncation and tailing analysis in microRNAs	Patel et al., 2016

tissue specific RNAi vectors also have recognized to be valuable for targeted gene silencing in particular plant tissues. The future work can be concentrated on developing superbly tuned RNAi based gene silencing vectors which are capable to operate in a spatially and temporally controlled manner. AmiRNA vectors are versatile and specific and thus they are recognized as second generation RNAi vectors (Djami-Tchatchou et al., 2017). miRNAs based manipulations have developed as a new technique for crop improvement for instance, genetic modification of agronomic traits and development of breeding strategies (Unver et al., 2009). We have discussed below, some more examples of the functions of newly identified miRNAs in different model crop plants (Table 2).

5. Role of miRNAs in Algae

miRNAs are extensively in plants, algae and animals, and their expression is regulated in a tissue-specific and time-dependent manner in species. Several studies have recognized the functions of miRNAs in cellular and biological processes (Wang et al., 2017). Usually, their functions have been found in cell differentiation, cell death, organ development and cell apoptosis (Liang et al., 2010). Unicellular green alga Chlamydomonas reinhardtii, is the first report of miRNAs in any single celled organism (Li et al., 2014; Willmann et al., 2007). In Saccharina japonica, miR8181 played an essential role in the regulation of "cell growth and development". This miRNA regulates the cell cycle, cell development and cell differentiation. miR8181 also play an important role in the regulation of ABC transporters, Hsp90, E3 ubiquitin protein ligase, SET2 and HAD superfamily hydrolases. In a study, they find out 55 target genes of miR8181 in S. japonica were primarily involved in glycolysis and gluconeogenesis (Yang et al., 2021).

In Chlamydomonas reinhardtii, cre-miR910 and cre-miR914 were found to be connected with various stresses such as UV-B, salinity and heat shock. In a study, found that endogenous miRNAs (cre-miR1158, cre-miR1150.3 and cre-miR1166.1) are responsive for sulphur deficiency in C. reinhardtii. In that experiment, found that the transgenic strains generated more hydrogen than wild type. This is the first study that shows miR1166.1 is highly expressed in algae, and that make it an excellent candidate for increasing bio-hydrogen production from algae (Anwar et al., 2019; Wang et al., 2019). According to that study, miR1166.1 was highly over-expressed after sulphur scarcity. Sulphur scarcity induces strong hydrogen production in C. reinhardtii. Therefore, it is recognized as hydrogen generation, regulating factors. C. reinhardtii, found some cre-miRNA such as cre-miR906-3p was upregulated, whereas cre-miR910 and cre-miR915 were downregulated under multiple stresses, which exhibit that these miRNAs potentially play an important role in the modulation of stress adaption in C. reinhardtii (Gao et al., 2016). Cre-miR906-3p also regulates the expression of ATP4 under UV-B radiation. Some researchers, found that cre-miR906-3p was upregulated under several stress conditions (UV-B, salinity and heat shock), which indicate that the growth and photosynthetic activity were elevated, and the ROS production and mortality rate was reduced in cre-miR906-3p overexpressing under stress. It played a positive role in the defense the cells in adverse conditions. Further, they studied the effects of various stresses on the expression of cre-miR910 and its target NCR2. Different exposure times of UV-B radiation caused the downregulation of cre-miR910, but significant overexpression of NCR2. The effects of salinity and heat shock on the expression of cre-miR910 were very similar to UV-B radiation. Enhancing the exposure times of heat shock levels and salinity caused the upregulation of defense system related genes NCR2 and downregulation of cre-miR910 expression (Gao et al., 2016).

6. Conclusion and Future directions

This review elaborates the finding about miRNAs and their function in targeting genes and TFs to restrict the abiotic stress effect in plants. It seems that theses miRNAs are crucial part of regulatory network that control pathways in response to abiotic stress, prominence their role in stress tolerance. In specific, miRNAs are essential transcriptional regulators of small RNA that control the important processes in plants such as growth, development, response and abiotic

Table 2. Functions of conserved miRNAs in model and crop plants.

S. N.	Plant species	miRNA	Target genes	Response	References
1	*Arabidopsis thaliana*	miR395	BnSultr, BnAPS	Transition in juvenile-adult vegetative phase delayed; surface trichomes absent or condensed	Huang et al., 2010
2	*Arabidopsis thaliana*	miR408	Copper related gene	vegetative development	Song et al., 2018
3	*A. thaliana*	miR399	IPS-1	Enhanced growth under phosphorus deficit; cold tolerance	Gao et al., 2015
4	*Oryza sativa*	miR393	Auxin receptor gene (TIR1 and AFB2)	Drought stress responsive	Zhou et al., 2010
5	*A. thaliana*	miR156	SBP/SPL	Transition between juvenile-adult phases of vegetative growth	Zheng et al.,2019
6	*O. sativa*	miR820	DRM2	Responsive to heat and salinity stress	Sharma et al., 2015a
7	*O. sativa*	miR167	ARF transcription factors	Cold stress	Jeong et al., 2011
8	*O. sativa*	miR319	TCP	Salinity and drought stress tolerance enhanced	Zhou et al., 2013
9	*O. sativa*	miR397	L-ascorbate oxidase	High temperature response and adaptation	Jeong et al., 2011
10	*O. sativa*	miR390	SRK	Boost in cadmium accumulation	Ding et al., 2016
11	*Vigna unguiculata*	miR156b, miR156f	Multicystati gene	Drought stress; protein degradation	Shui et al., 2013
12	*Glycine max*	miR156, miR160	Squamosa binding protein	Seed growth	Song et al., 2011
13	*Glycine max*	miR394a	F-box Protein	Greater drought tolerance	Ni et al., 2012
14	*Glycine max*	miR164, miR166	ARF transcription factors	Response in development of seed	Song et al., 2011
15	*Glycine max*	miR172	AP2 like TFs	Higher drought and salinity tolerance	Li et al., 2016
16	*Hordeum vulgare*	miR156d	Squamosa binding protein	Drought stress; plant developmental process	Curaba et al., 2012

Table 2 Cont...

17	*H. vulgare*	MiR396d	Growth factor	Expansion of seed	Shuzuo et al., 2012
18	*A. thaliana*	miR160	ARF transcription factors ARF10, ARF16, and ARF17	Heat tolerance	Lin et al., 2018
19	*Zea mays*	miR167	ARF transcription factors	Stress retort	Sheng et al., 2015
20	*Triticum aestivum*	miR395	ATP sulfurylase genes	Abiotic stress response	Han et al., 2013
21	*Arachis hypogaea*	miR156	Squamosa binding protein	Plant development	Chi et al., 2011
22	*Ipomoea batatas*	miR160, miR164, miR166, miR398	ARF, NAC1 transcription factors	Root (fibrous) storage and growth	Sun et al., 2015
23	*Solanum tuberosum*	miR475	Thioredoxi	Metabolism	Din et al., 2014

stress tolerance. Though, due to the complexity of miRNAs regulatory processes, the knowledge of the regulating mechanism of action is still limited in present. A deeper study on the miRNA's role in response to plant stress is needed. Though huge progress has been made over the past twenty years, within the identification of both protein-coding genes and small RNAs responsive to MicroRNAs for improving plant tolerance to abiotic stress by abiotic stress, all of these studies are still in their infancy and, therefore, more time is needed before miRNAs become a real target for improving crop tolerance.

The application of RNAi-mediated gene silencing has generated many successful transgenic crop examples with developed tolerance against abiotic stress factors. Recently, it has been revealed that the RNA silencing pathways play a role in both abiotic and biotic stress responses in plants. The RNA silencing based technologies will support humankind to confront the challenges of productive farming in the rising adverse environmental conditions linked with weather changes. With the recognition of the miRNA alternation potential as a believable tool in plant improvement, it is also essential to be aware that such genetic modification ways can lead to unexpected side effects. If the miRNA expression or the target gene is changed, it can possibly result the unwanted pleiotropic changes in plant morphology and development. Consequently, it is essential to understand the miRNA regulation mechanisms in the plant growth and development or plant responses to several abiotic stresses. This will facilitate the project of suitable strategies subsequent in the desired traits, but with least trade-offs in the altered crops. CRISPR (clustered regularly interspaced short palindromic repeats) driven modulation of miRNA expression will help in functional characterization of biotic and abiotic stress associated miRNA in plants. CRISPR also can be used to mend the stress tolerance by alteration and modification of miRNAs via development of miRNA edited lines of plants. The machine learning technique can also be used to predict plant abiotic stress through having the plant miRNA expressions. Therefore, a more comprehensive study in future will be useful to develop better approaches for enhancing abiotic stresses in plants.

7. Conflict of interest

The authors state that they have no conflict of interest.

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