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DROUGHT-RESPONSIVE miRNAs IN PLANTS: A REVIEW

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Abstract

Review paper

MicroRNAs (miRNAs) are known as single-stranded RNA molecules that are functional in all steps of plant life including growth, development, and stress responses. Plant genomes harbor hundreds of miRNAs, which have diverse functions in regulating numerous biological processes. After being first discovered in plants in the year 2002, thousands of plant miRNAs have been identified so far. With the help of recent advances in high-throughput sequencing technologies, genome and transcriptome-wide screening of miRNAs in specific conditions and a variety of plants have been conducted. Among the challenging conditions that adversely affect plants, drought stress is one of the main factors limiting plant growth and productivity worldwide. So far, drought-responsive miRNAs have been uncovered in particular plants. Moreover, functional characterizations of some miRNAs provide insights into their role in drought regulatory mechanisms. This review summarizes the most recent findings on miRNA-based drought stress regulation of plants. The study provides insights into the role of miRNAs in the drought stress response of the plant.

Keywords: *Drought; gene regulation; miRNA; plant response; tolerance.*

BİTKİLERDE KURAKLIĞA DUYARLI miRNA'LAR: DERLEME

Özet

Derleme makale

MikroRNA'lar (miRNA'lar), bitki yaşamının büyüme, gelişme ve stres yanitlari olmak üzere tüm aşamalarinda fonksiyonel olan tek iplikli RNA molekülü olarak bilinir. Bitki genomları, sayısız biyolojik süreci düzenlemede çeşitli fonksiyonlari olan yüzlerce miRNA'yı barındırır. Bitkilerde ilk kez 2002 yılında keşfedildikten sonra, bugüne kadar binlerce bitki miRNA'sı tanımlanmıştır. Yüksek verimli dizileme teknolojilerindeki son gelişmelerin yardımıyla, belirli koşullardaki çeşitli bitkilerde miRNA'ların genom ve transkriptom düzeyinde taranması gerçekleştirilmiştir. Bitkileri olumsuz etkileyen koşullardan kuraklık stresi, dünya çapında bitki büyümesini ve üretkenliğini sınırlayan başlica faktörlerden biridir. Bugüne kadar, belirli bitkilerde kuraklığa duyarlı miRNA'lar ortaya çıkarılmıştır. Ayrıca, bazı miRNA'ların fonksiyonel karakterizasyonları, kuraklığı düzenleyici mekanizmalardaki rolleri hakkında bilgi sağlamaktadır. Bu derleme, bitkilerin miRNA tabanlı kuraklık stresi regulasyonuna ilişkin en son bulguları özetlemektedir. Çalışma, bitkinin kuraklık stresi yanıtında miRNA'ların rolü hakkında fikir vermektedir.

Anahtar Kelimeler: *Bitki yanıtı; gen regulasyonu; kuraklık; miRNA; tolerans.*

1 Introduction

Drought stress is one of the main factors restricting plant growth and productivity worldwide. About half of the Earth's land area is affected by the drought [1]. According to the International Disaster Database (EM-DAT), more than 11 million people died, and 2 billion people were affected due to drought between 1900 and 2011 [2]. It is predicted that these conditions will worsen with the effect of global warming [3]. Therefore, deciphering plant responses against drought stress and understanding the molecular mechanisms of how plants naturally combat this stressor is of critical importance.

MicroRNAs (miRNAs) are a class of non-coding small RNAs with an average length of 21 nucleotides (about 20-24 nucleotides). By binding to their complementary mRNA target in the cytosol, they can suppress the gene expression at the post-transcriptional level and regulates the biological processes. In plants, perfect or partial complementarity of miRNA result in the cleavage of the target mRNA [4-6], and thereby suppresses translation and gene function (Figure 1). Since their first discovery in *Caenorhabditis elegans* [7], 38,589 miRNAs have been currently registered in the miRNA database, miRBase v22.1 (http://www.mirbase.org) [8]. In addition, PmiREN (Plant miRNA ENcyclopedia) contains 20,388 miRNAs belonging to 5,757 families (HTTP://WWW.PMIREN.COM) [9].

Over the last two decades, miRNAs have been identified as one of the key players in the process of

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detecting and responding to drought in plants. The development of high-throughput sequencing approaches such as transcriptome (mRNA) or small RNA (sRNA) sequencing improved our knowledge of miRNA identification.

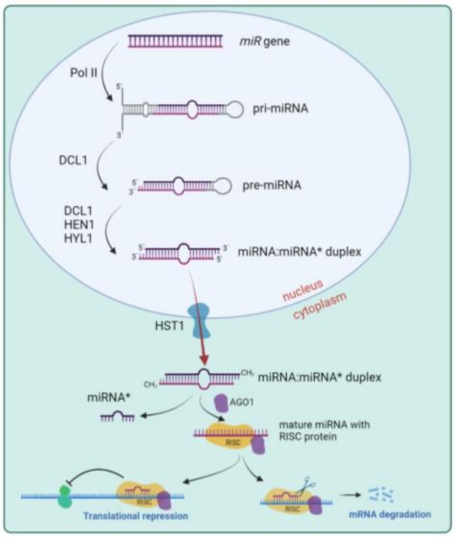

Figure 1. miRNA biogenesis in plant cell.

MIRNA genes (***miR* genes**) are transcribed by RNA polymerase II enzyme (Pol II). By means of the complementary sequences, the transcript forms a stem-loop structure, called as primary or **pri-miRNA**. The main enzyme transforming pri-miRNA to **pre-miRNA** is Dicer-like 1 (DCL1), which is an RNase III endonuclease. It also catalyzes the formation of **miRNA:miRNA* duplex** with the aid of accessory proteins including the double-stranded RNA-binding protein Hyponastic Leaves 1 (HYL1) and small RNA methyltransferase HUA Enhancer 1 (HEN1), which methylates the 2` OH groups. The methylated miRNA/miRNA* duplex is exported to the cytosol by nuclear membrane localized Hasty protein (HST1). Once Argonaute (AGO1) and RNA-induced silencing complex (RISC) proteins selectively assembled with the guide strand (miRNA), the complementary strand or the passenger strand (miRNA*) leaves and degrades. The mature miRNA strand binds a complementary transcript in the cytosol and forms a double stranded mRNA, which either blocks the translation process called as translational repression or cause mRNA degradation.

In the last two decades, transcriptome sequencing has identified drought-responsive miRNAs in a variety of plant species including *Arabidopsis* [10], potato [11], rice [12], soybean [13], maize [14], *Populus trichocarpa* [15], *Cynanchum komarovii* [16], *Citrullus colocynthis* [17], *Brassica napus* [18], barley [19] and wheat [20]. Although the plant genome harbors hundreds of miRNA-coding genes, their expressions are tissue or developmental stage-specific [21]. Moreover, it has been found that a single miRNA can target hundreds of mRNAs pointing out their comprehensive role in gene regulation [22]. In addition to those studies, small RNA sequencing technology has been successfully applied to identify drought-responsive miRNAs, as in rice [23], wheat [24], peach [25], sugarcane [26], *Medicago truncatula* [27], and potato [28]. Recently, an integrated drought-responsive mRNA and miRNA analyses were conducted by constructing mRNA and small RNA libraries in tobacco [29], tomato [30] and grapevine [31]. Akdogan et al. [32] found tissue-specific differentially expressed miRNAs in drought-sensitive and drought-tolerant wheat cultivars. According to this study, miR156, miR167, miR319, miR398, miR5083, and miR5174 were differentially expressed in leaves; while miR164, miR399, miR4393, miR5072, and miR8006 were differentially expressed in roots upon drought stress treatment. Other key molecule aquaporins are found in the plasma and intracellular membranes of plant cells which are channel proteins divided into four subfamilies: plasma membrane intrinsic proteins (PIPs), tonoplast intrinsic proteins (TIPs), NOD26-like intrinsic proteins (NIPs) and small basic intrinsic proteins (BIPs). The expression of aquaporin-encoding genes can be regulated to help plants maintain their water balance under drought stress conditions [33]. To explore miRNAs and assess the expression of genes involved in drought stress tolerance, leaf and root expression sequence tags (ESTs) were analyzed in barley. The highest up-regulation was observed from the aquaporin family HvPIP1:4 [19]. These studies but not limited to, revealed novel and drought stress-responsive miRNAs in plants. However, plant species, tissue specific and developmental stage variations among those experiments limit uncovering global drought stress responsive miRNAs. While these studies give a broad perspective to decipher stress-responsive miRNAs, they give either up-regulated or down-regulated miRNAs which exhibit limited information for their key functions. Instead, functional studies reveals impressive results about the roles of these molecules in drought response regulation.

2 miRNA-Targeted Transcription Factors

In a global overview, drought stress-responsive miRNA studies revealed key miRNA molecules involved in drought stress regulation of plants. miRNAs generally participate in this bioprocess by targeting transcription factors (TFs) such as MYB (myeloblastosis), ARF (Auxin response factor), and NFY-A (nuclear transcription factor Y subunit alpha). For instance, in *Arabidopsis*, abscisic acid (ABA) induces miR159 accumulation during drought at the germination stage and miR159, as a negative regulator causes the cleavage of its target transcripts, *MYB101* and *MYB33*, to suppress hormone signaling (Table 1) [34, 35]. MYB transcription factors, as being the key TFs in controlling the development and stress regulation, binds *cis* elements in the *RD22* (*dehydration-responsive gene response to dehydration 22*) promoter and promote its expression resulting in osmotic and drought stress tolerance in transgenic *Arabidopsis* [36, 37]. By contrast, miR169a and miR169c are down-regulated by drought stress. Expression of miR169-target transcript *NFYA5* (encoding a subunit of the nuclear factor Y (NF-Y) transcription factor) increases and leads to enhanced drought resistance in *Arabidopsis* [38]. In addition, miR169 functionality in drought stress response has been found in rice [39], *Medicago truncatula* [27], tomato [40, 41], and wheat [16]. By contrast, miR169g was upregulated by drought in rice, and the existence of two proximate DREs (dehydration-responsive element) in the upstream of the miR169g suggests the role of miR169g in drought stress response [39]. In addition, transgenic tomato plants overexpressing miR169c conferred drought tolerance by reducing stomatal conductance and water transpiration rate [40]. A recent study found that overexpression of soybean miR169c targeting *NF-YA* enhanced drought stress sensitivity in Arabidopsis [42]. It is found that is a negative regulator in drought stress and its expression is induced by polyethylene glycol (PEG), high salt, cold stress and ABA in a wide range of soybean tissues.

NAC (NAM, ATAF, and CUC) transcription factors are a plant-specific family involved in multiple developmental and stress regulatory processes, as positive or negative regulators [43, 44]. Overexpression of a mutant NAC2 gene which is unable to target by miR164b enhanced drought and salt tolerance of rice seedlings [45]. The study suggests that miR164b is a positive regulator in drought resistance. Another study found that overexpression of miR164-targeted NAC transcription factors, namely *Oryza miR164-targeted NAC* (*OMTN1–OMTN6*), increased the drought stress susceptibility in rice seedlings [46]. In addition to these TFs, miR1119 targeted *bHLH* (*basic helix–loop–helix*), *LZ* (*leucine zipper*), and *CS* (*CTP synthase*) in wheat (*Triticum aestivum*) are found to be involved in drought stress regulation. Overexpression of miR1119 improved drought stress tolerance of wheat [47].

Auxin response factors (ARFs) are the transcription factors involved in every aspect of plants life including developmental and stress-regulatory bioprocesses [48]. miRNAs-mediated regulation of *ARFs* genes has been shown in some studies. For instance, overexpression of ARF-targeting miR393 improved drought stress tolerance in creeping bentgrass plants [49]. Also, *WD40* (*tryptophan-aspartic acid (W-D) repeat*), *HD-Zip* (*Homeodomain-Leu zipper*), and *AP2* (*Apetala-2*) are the other known transcription factors (TFs) that are targeted by different miRNAs and involved in the drought tolerance mechanisms (Table 1). Arshad et al. [50] showed that overexpression of WD40-targeting miR156 reduced water loss and improved root growth under drought stress in *Medicago sativa* seedlings. Zhang et al. [51] indicated that knockdown of miR166 which targets the HD-Zip transcription factor confers drought stress tolerance by maintaining reduced stomatal conductance and transpiration rates in rice (*Oryza sativa*). These studies show a strong interaction between miRNA and TFs in the homeostasis of drought stress regulation.

3 miRNA and Hormone Homeostasis in Drought Response

Reduction in cell growth is another strategy to struggle with water deficient condition. Because it directs the energy required for growth into protective molecules to combat stressors [52]. In this process auxin hormone signaling is found to be controlled by some miRNA families that help adaptive plant survival under many stress conditions, including drought. For instance, miR393 was accumulated in drought stressed *Arabidopsis* [53], populus [54], wheat [55], rice [56], and sugarcane [57]. But it is important to note that miR393 is a global stress responsive miRNA related to auxin signaling in which it accumulates under biotic and abiotic stress conditions such as bacterial infection [58], salt [59], UV-B [60], cold and heat [61]. Upregulation of miR393 degrades its target transcript *TIR1* (transport inhibitor response 1), an auxin receptor. As an enzyme, TIR1 degrades the Auxin/indole-3-acetic acid (Aux/IAA) proteins. In the cell, ARF and Aux/IAA heterodimerization activates the auxin-responsive genes. Degradation of *TIR1* by increased miR393 expression prevents the Aux/IAA-ARF heterodimerization, resulting in inhibition of auxin signaling [61]. Therefore, increased miR393 expression by drought stress contributes to the suppression of ARF-mediated gene expression leading to a recession in plant cell growth and development.

In addition to miR393, miR160 and miR390 participate in the auxin-mediated drought stress response and tolerance mechanisms. Interestingly, miR390 does not target a protein coding transcript, instead, it stimulates the generation of *TAS3* tasiRNA (TAS3-derived *trans*-acting small interfering RNA), which controls auxin-mediated organ (aerial laterals) polarity establishment by targeting *ARF2*, *ARF3*, and *ARF4* TFs [62-65].

Another phytohormone that regulates drought-stress response is abscisic acid (ABA). miRNAs play role in the drought stress regulation by involving in the biosynthesis of ABA and signaling. Most recently, Gao et al. [96] demonstrated the importance of a bZIP family transcription factor, *OsbZIP86*, for drought-induced ABA biosynthesis in rice (*Oryza sativa*). In the absence of drought, it was shown that *OsbZIP86* is post-transcriptionally suppressed by miR2105 and ABA synthesis remains at low level. Generation of *OsbZIP86* overexpression and *miR2105* downregulation/knockout lines result in enhanced ABA synthesis and plant drought resistance without any yield suppression.

Another study found that serrate (SE), an eukaryotic RNA processing factor functional in miRNA processing [97], acts as a negative regulator in drought resistance of apple (*Malus domestica*) by regulating the expression of MYB transcription factors and miRNAs. SE suppresses the expression of two MYBs, namely *MdMYB88* and *MdMYB124* transcripts, which directly regulate the expression of 9-cis-epoxycarotenoid dioxygenase 3 (*MdNCED3*) gene, encodes for a key enzyme in abscisic acid (ABA) biosynthesis. In addition, SE plays role in the biogenesis of some positive (miR156, miR166, miR172, and miR319) and negative (miR399) regulator of drought stress [98]. However, the functional characterization of these miRNAs in apple has not been completed yet.

4 Functional Identification of Drought-Stress Responsive miRNAs

In addition to hormonal control of drought stress response via miRNAs, some studies reported that plant drought stress tolerance was gained by miRNA overexpression. For instance, miR396a overexpression in *Arabidopsis* suppresses *GRF* (growth-regulating factor) level and result in lower densities of stomata and drought tolerance than that of wild-type plants [10]. In addition, the same results have been observed in tobacco in which *Arabidopsis* miR396 overexpression enhanced plant drought tolerance [78]. Previous reports revealed that miR166 is another drought stress-responsive miRNA. Its expression decreased under drought stress in *Triticum dicoccoides* [55], barley [87] and alfalfa [88]. Overexpression of miR166a in alfalfa regulated the root and nodule development and hence drought tolerance response [88]. Controversially, drought stress decreased miR166 accumulation in alfalfa [90].

Other than those global miRNAs responsive to drought stress, experimental studies proved that some unique plant miRNAs are drought associated and enhanced drought tolerance when overexpressed. For instance, Os-miR319a overexpression in transgenic creeping bent grass (*Agrostis stolonifera*) increased drought and salt tolerance [69].

In chickpea, increased drought tolerance was achieved by overexpression of miR408 [80], which in turn is known as environmental regulator in a variety of stresses such as dehydration [87, 90, 32], and mechanical stress [91], and reactive oxygen species [92]. In line with this study, recently Balyan et al. [99] found that over-expression of miR408 in drought-sensitive rice enhances photosynthetic parameters such as electron transport rate (ETR) and effective photochemical quantum yield of photosystem II (Y(II)) and water scarcity tolerance. Additionally, the function of miR408 in drought-stress tolerance has been recently validated in cowpea seedlings, where overexpression of miR408 result in enhanced drought and salinity tolerance in transgenic lines compared to the wild type [100]. These studies revealed the importance of miR408 in providing drought resistance in plants.

Kang et al. [66] showed that salt and drought stress tolerance was achieved in tobacco plants after miR156 overexpression. Similarly, another study by Feyissa et al. [67] highlighted the importance of miR156 in the drought stress regulation in alfalfa (*Medicago sativa*). The study indicates that drought tolerance is controlled via the interaction of miR156 and squamosa-promoter binding protein-like (SPL) transcription factors (*SPL13*). However, it is stressed that higher miR156 overexpression increases drought susceptibility in alfalfa.

Another miRNA regulates drought stress tolerance is miR171. Independent studies by Wang et al [93] and Um et al [94] showed that miR171/SCARECROW-LIKE (SCL) module regulates drought stress response in apple (*M. domestica*) and rice (*O. sativa*). While increased drought tolerance was achieved by induction of antioxidant gene expression and ascorbic acid metabolism in apple (Wang et al. 2020), it was achieved through regulation of flavonoid biosynthesis genes in rice (Um et al. 2022). In addition to these studies, miRNAs functionally characterized in drought stress regulation are summarized in Table 1.

Table 1. Functionally characterized drought-responsive miRNAs.

miRNA family	Species	Target	Result	Reference
miR156	*Zea mays*	SPL	Overexpression improved drought and salt tolerance in tobacco	Kang et al. [66]
miR156	*Medicago sativa*	SPL	miR156 has a role in drought stress regulation. However, high expression increases drought susceptibility in alfalfa (*M. sativa*)	Feyissa et al. [67]
miR156	*Medicago sativa*	WD40	Overexpression reduced water loss, and enhanced root growth under drought	Arshad et al. [50]
miR159	*Arabidopsis thaliana*	MYB	Positive regulator in ABA signaling. Drought tolerance	Reyes and Chua [34]
miR164	*Oryza sativa*	NAC	Drought tolerance	Fang et al. [46], Jiang et al. [45]
miR166	*Oryza sativa*	HD-Zip	Knockdown confers drought stress tolerance, by maintaining reduced stomatal conductance and transpiration rates	Zhang et al. [51]
miR169	*Arabidopsis thaliana*	NF-Y	Overexpression increased water loss in leaves, and more sensitive to drought stress	Li et al. [38]
miR169	*Solanum lycopersicum*	NF-Y	Overexpression led reduction in stomatal opening, transpiration rate, and leaf water loss; while improved drought tolerance	Zhang et al. [40]
miR169	*Glycine max*	NF-Y	Overexpression increased drought stress sensitivity in *A. thaliana*	Yu et al. [42]
miR171	*Malus domestica*	SCL26.1	Knockout improved drought stress tolerance in apple	Wang et al. [2020]
miR171	*Oryza sativa*	SCL6-I and SCL6-II	Expressed under drought stress and regulates the expression of *SCL6-I* and *SCL6-II.* Overexpression led reduced drought symptoms.	Um et al. [2021]
miR172	*Glycine max*	AP2	Overexpression confers drought and salt tolerance in *A. thaliana*	Li et al. [68]
miR319	*Oryza sativa*	TCP	Overexpression enhanced drought and salt tolerance in bent grass (*Agrostis stolonifera*)	Zhou et al. [69]
miR393	*Oryza sativa*	Auxin receptor genes (*OsTIR1* and *OsAFB2*)	Hyposensitivity to synthetic auxin-analog, less tolerance to salt and drought	Xia et al. [70]
miR393	*Oryza sativa*	ARF	Overexpression improved drought stress tolerance in creeping bent grass	Ho et al. [71]
miR393	*Hordeum vulgare*	ARF	Overexpression increased stomatal density with decreased guard cell length, more sensitive to drought stress. Knockdown enhanced drought tolerance	Yuan et al. [72]

Table 1. Functionally characterized drought-responsive miRNAs. (Continued)

miR394	*Setaria italica*	FBP6	Overexpression increased drought tolerance in *A. thaliana*	Geng et al. [73]
miR394	*Glycine max*	*Glyma08g11030*	Overexpression lowered leaf water loss, enhanced drought tolerance in *A. thaliana*	Ni et al. [74]
miR396	*Arabidopsis thaliana*	*GRF*	Overexpression reduced stomata density and increased drought tolerance	Liu et al. [75]
miR397	*Glycine max*	*PPR*	Overexpression reduced drought resistance in soybean with dwarf and thick cell wall phenotypes.	Sun et al. [76]
miR396	*Glycine max*	GRF	Overexpression led lower water level in leaves with lower survival rate in *A. thaliana*	Liu et al. [77]
miR396	*Arabidopsis thaliana*	GRF	Overexpression decreased water loss and increased relative water content and drought tolerance in tobacco	Yang and Yu [78]
miR398	*Glycine max*	CSD, CCS	Increased sensitivity to drought in *G. max*	Zhou et al. [79]
miR398	*Glycine max*	CSD, CCS	Increased sensitivity to drought in *A. thaliana*	Zhou et al. [79]
miR408	*Cicer arietinum*	*plantacyanin*	Overexpression increased drought tolerance	Hajyzadeh et al. [80]
miR408	*Oryza sativa*	-	Enhanced drought resistance, improved relative water content (RWC), lower electrolyte leakage (EL), and less lipid peroxidation in ryegrass (*Lolium perenne* L.)	Hang et al. [81]
miR408	*Arabidopsis thaliana*	*Plantacyanin, Uclacynin, Cupredoxin, Lac3*	Overexpression improved tolerance to salinity, cold and oxidative stress, while enhanced sensitivity to drought and osmotic stress	Ma et al. [82]
miR408	*Oryza sativa*	*phytocyanins, Aux/IAA*	Overexpression confers cold tolerance, while decreased drought tolerance	Sun et al. [43]
miR408	*Oryza sativa*	*Plantacyanin, pirin, etc.*	Overexpression of in drought-sensitive rice enhances photosynthetic parameters and water scarcity tolerance	Balyan et al. 2022
miR408	*Vigna unguiculata*	*Laccase 3 (LAC3), Laccase 12 (LAC12)*	Overexpression enhanced drought and salinity tolerance	Mishra et al. 2022
miR535	*Oryza sativa*	SPL	Overexpression increased drought stress sensitivity in *O. sativa*	Yue et al. [83]
miR827	*Arabidopsis thaliana*	SPX	Constitutive expression negatively affected plant water use efficiency, time to anthesis and grain weight of *H. vulgare*	Ferdous et al. [84]
miR827	*Hordeum vulgare*	SPX	Overexpression under the control of drought-inducible promoter improved water use efficiency in *H. vulgare*	Ferdous et al. [84]
miR1119	*Triticum aestivum*	bHLH, LZ, CS	Overexpression improved drought stress tolerance	Shi et al. [85]
miR1916	*Solanum lycopersicum*	HDAC, STR	Overexpression increased drought sensitivity. Silencing improved drought-resistance in tomato and tobacco.	Chen et al. [86]
miR2105	*Oryza sativa*	*OsbZIP86*	*OsbZIP86* overexpression and miR2105 downregulation/knockout lines revealed enhanced ABA synthesis and plant drought resistance without any yield suppression	Gao et al. [96]
miR5505	*Oryza sativa*	Multiple targets	Overexpression led drought and salt stress tolerance	Fan et al. [95]

5 Conclusion

MicroRNAs are important players in most of the abiotic stress regulation mechanisms in plants. Therefore, identification and functional characterization of miRNAs is critical to understanding the molecular regulation mechanisms of plants to combat with water scarcity, a common problem all around the world. A Recent development in genome or transcriptome-based miRNome analyses increased our understanding on miRNA-drought stress regulation. Also, machine learning studies can help to find out the most important miRNAs in various abiotic stress conditions. Genetic modification on miRNAs by using CRISPR-Cas9 (clustered regularly interspaced short palindrome repeats-CRISPR-associated protein 9) and molecular cloning are promising approaches to generate drought-tolerant plants. In addition, the identification of drought-responsive miRNAs provides an opportunity for early detection of plant drought resistance by using miRNA-based biosensors. This review exhibits the most recent functional findings on miRNA-drought regulation. The represented miRNAs can be the promising target for molecular breeding studies.

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