American Journal of Plant Sciences, 2014, 5, 748-759
Published Online March 2014 in SciRes. http://www.scirp.org/journal/ajps
http://dx.doi.org/10.4236/ajps.2014.55089

MicroRNAs: The Potential Biomarkers in Plant Stress Response

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Received 20 January 2014; revised 24 February 2014; accepted 11 March 2014

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Abstract

MicroRNAs (miRNAs) are endogenous small RNA regulatory molecules of approximate 20 - 24 nucleotides that are involved in regulating the intrinsic growth and development of organs in plants and animals as well as in maintaining the integrity of genomes. Past few years have witnessed an increase in research reports on the crucial role of miRNAs in plant stress response. Plant miRNAs regulate gene expression at the post-transcriptional level not only by suppression of mRNA translation but also by direct cleavage of the target mRNAs. This review starts with a brief overview on small RNAs including miRNAs, biogenesis of miRNA and focuses mainly on the various up- and down-regulated plant miRNAs under different biotic and abiotic stresses showing advancement of studies about miRNA and their stress regulation pathway. This review explores the emerging role of miRNAs as potential biomarkers in plant stress responses.

Keywords

MicroRNAs; Biomarker; Plant Stress Response

1. Introduction

Plants encounter various biotic and abiotic stresses which greatly affect their growth, development and yield. Since plants are sessile in nature so, they have evolved sophisticated mechanisms and efficient strategies to withstand the environmental stresses which are caused by various biotic or abiotic factors. The different mechanism of stress response contributes to stress resistance or stress tolerance at different morphological, biochemical and molecular levels [1]. The advancement of molecular biology research has shown that plants respond to stress not only at the mRNA or protein level but also at the post transcriptional level [2]. The small RNAs (sRNAs) are the bioregulators of plant stress response, regulates by transcriptional gene silencing (TGS)

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How to cite this paper: Bej, S. and Basak, J. (2014) MicroRNAs: The Potential Biomarkers in Plant Stress Response. *American Journal of Plant Sciences*, **5**, 748-759. http://dx.doi.org/10.4236/ajps.2014.55089

or post-transcriptional gene silencing (PTGS) [3]. They perform gene silencing by RNA slicing [4], translational repression [5], histone modification and DNA methylation [6] [7]. Plant sRNAs are complex in nature and are classified on the basis of their biogenesis and the structure of the genomic loci [2]. sRNAs include microRNAs (miRNAs), small interfering RNAs (siRNAs), piwi interacting RNAs (piRNAs), small temporal RNAs (stRNAs), tiny non-coding RNAs (tncRNAs) and small modular RNAs (smRNAs). Among the complex variety of sRNAs, the microRNAs have been extensively characterized and found to be involved in various stress responses. They are encoded by MIR genes and are the key molecules in gene regulatory networks. Plant miRNA plays a vital role in development, physiological processes and stress responses. Many stress-regulated genes are found to be regulated by miRNAs. This review gives an overview of miRNAs, biogenesis of miRNAs and their roles as potential biomarkers in response to different biotic and abiotic stresses.

2. MicroRNAs: Tiny Size yet Significant Role

MicroRNAs are endogenous, single stranded non-coding regulatory RNAs of about 20 - 22 nt in size, are encoded by MIR genes. MicroRNA (miRNAs) lin-4 was first discovered in *Caenorhabditis elegans* in 1993 [8] [9] but the term microRNA was coined in 2001. They regulate various developmental and physiological processes [10]. Plant miRNAs are involved in developmental, metabolic processes, pattern formation, hormone regulation, biotic and abiotic stress response and in the pathway of self-regulation of the miRNA biogenesis [11].

2.1. MicroRNA Biogenesis

In the miRNA biogenesis pathway, the primary miRNAs (pri-miRNAs) containing a long sequence of several hundred nucleotides gets transcribed from MIR genes (nuclear-encoded) by the RNA polymerase II enzyme (Pol II) [12]. The pri-miRNA forms a characteristic hairpin structure. The pri-miRNAs are then processed into pre-miRNAs catalyzed by RNase-III like enzymes called Dicer-Like (DCL1) and HYPONASTIC LEAVES 1(HYL1) and SERRATE (SE) proteins [13]. The pre-miRNA hairpin precursor gets converted into a 20- to 22-nt miRNA/miRNA* duplex where methylation occurs at the 3’ terminus by HUA ENHANCER 1 (HEN1). An exportin protein HASTY (HST1) exports it into the cytoplasm [13]. While entering the cytoplasm one of the duplex strands of miRNA is directed to the exosome and degraded by Small RNA Degrading Nuclease (SDN) [14]. The mature miRNA gets exposed to RNA-induced silencing complex (RISCs) complex. It gets incorporated into an ARGONAUTE (AGO) protein which guides it to bind to the target transcripts on basis of sequence complementarity.

2.2. MicroRNA Mediated Regulation

MicroRNAs regulates gene expression either by target mRNA cleavage or by translational repression [15] [16]. The perfect pairing between mRNA and miRNA results in target mRNA cleavage whereas imperfect pairing results in repression. Plant miRNA mediates target mRNA cleavage. Recently, researchers have found a new miRNA-mediated regulation known as miRNA mediated mRNA decay. When there is partial or little similarity between target mRNA and miRNA, the miRNA decays the target mRNA by removing its poly (A) tail, making it unstable leading to decay [15] [17] [18].

2.3. MicroRNA Role in Plant Stress Response

Recent advancement on miRNA research has revealed their vital role in post transcriptional regulation of genes which are necessary for stress response [1]. MicroRNAs (miRNAs) are differentially regulated under various stresses. Certain miRNAs are either under or over-expressed or new miRNAs gets synthesized under stress. In plants various biotic and abiotic stress-regulated miRNAs have been identified and characterized. Mostly miRNA target genes which encodes various transcriptional factors or functional enzymes having important roles in abiotic stress response.

3. Potential miRNAs Biomarkers in Biotic Stress

3.1. Bacterial Infection

In Arabidopsis, miR393 induced by a bacterial pattern associated molecular pattern (PAMP) was found to be the first miRNA to have role in plant antibacterial pattern triggered immunity (PTI) which negatively regulates the auxin signaling pathway [19]. Three miRNAs—miR160, miR167 and miR393 were found to be highly induced while miR825 was found to be down regulated after infection with *Pseudomonas syringae* pv. Tomato (DC3000hrcC) [20]. miR398 was also found to be down regulated on bacterial infection [21].

3.2. Viral Infection

Turnip mosaic virus (TuMV)-encoded RNA silencing repressor P1/HC-Pro has been found to have link with miR171. In Arabidopsis, P1/HC-Pro induced miR156 and miR164 was reported [22] [23]. A novel miRNA, brassica-miR1885 was found to be induced by TuMV infection [24]. In Tomato Leaf Curl Virus (ToLCV) miR159 was found up regulated while miR164 and miR171 was reported down regulated [25]. In a study, the miR159/319 and miR172 were found as potential biomarkers for Tomato leaf curl New Delhi virus (ToLCNDV) infection [26]. The role of individual miRNAs in response to viral infection has not yet been reported.

3.3. Fungal Infection

10 miRNA families were differentially expressed in response to infection by the rust fungus *Cronartium quercuum f. sp. Fusiforme* which causes fusiform rust disease in loblolly pine trees [27]. In powdery mildew disease of wheat caused by fungus *Blumeria graminis f. sp.tritici* (Bgt) have showed miRNA differential expression patterns- miR156, miR159, miR164, miR171 and miR396, were found to be down regulated while miR393, miR444 and miR827 were found to be up regulated [28]. Overexpression of Osa-miR7696 was found in rice blast infection [29].

3.4. Nematode Infection

In response to *Heterodera schachtii* infection, miR161, miR164, miR167a, miR172c, miR396a, b and miR398a were found down regulated in Arabidopsis [3] [30]. In soyabean, 101 miRNAs belonging to 40 families were found to be responsive to the infection of the soybean cyst nematode *Heterodera glycines* [31]. **Table 1** lists important miRNAs differentially regulated under biotic stress conditions.

4. Potential miRNAs Biomarkers in Abiotic Stress

4.1. Oxidative Stress

The various environmental stresses—salinity, heavy metals, UV radiation, drought results in the rapid accumulation of reactive oxygen species (ROS) which includes superoxide radicals (O_2^-), hydrogen peroxide (H_2O_2) and hydroxyl radicals (OH^-) causes oxidative damage to the cells [32] [33].

Superoxide dismutases (SODs) convert the highly toxic superoxide radicals (O_2^-) into less toxic hydrogen peroxide (H_2O_2) [34]. The up regulation of the two Cu-Zn superoxide dismutase (CSD) genes were reported to be dependent on miR398 levels. The cytosolic CSD1 and plastidic CSD2 both are targeted by miR398. Under stress, the expression of miR398 is down regulated resulting in increased accumulation of CSD1 and CSD2 mRNAs resulting in reduced accumulation of the highly toxic superoxide free radicals [21] [35]-[37] (**Figure 1**).

In Arabidopsis, the miR398 family is represented by two members with three loci—MIR398a, MIR398b and MIR398c [2] [38]-[40]. A study has identified seven H_2O_2-responsive miRNAs—miR169, miR397, miR528, miR827, miR1425, miR319a.2 and miR408-5p in rice seedlings [41].

4.2. Drought Stress

Drought the most dominant abiotic stress caused due to shortage in precipitation, soil water deficiency and excess of evaporation [42]. Plants tolerate drought conditions by enhanced water uptake, reduced water loss and by other mechanisms [32]. Recent studies on *Triticum dicoccoides* [43], cowpea [44], soybean [45], *Phaseolus vulgaris* [46], and tobacco [47] have found differential expression patterns of miRNAs in relation to drought stress. In Arabidopsis, miR396, miR168, miR167, miR165, miR319, miR159, miR394, miR156, miR393, miR171, miR158, and miR169 were found in response to drought [48] where miR393, miR319, and miR397 were up regulated [39]. miR393 up regulation is linked to drought stress, it decreases the TIR1 levels which is a positive regulator of growth and development and hence, results in retardation in growth. In rice, miR169g, miR171a and miR393 were found to be induced in response to dehydration [49]-[51]. It was found that the

Table 1. The potential miRNA biomarkers identified in different biotic stress conditions.

Type of Stress	miRNA biomarkers	Up regulated	Down regulated	References
Virus	miR171		⇩	Kasschau *et al.* 2003, Zhou and Luo 2013
	miR156, miR164	⇧		Kasschau *et al.* 2003
	miR159	⇧		Naqvi *et al.* 2008
	miR164, miR171		⇩	
	miR1885	⇧		He *et al.* 2008
Bacteria	miR393	⇧		Navarro *et al.* 2006
	miR398		⇩	Jagadeeswaran *et al.* 2009
	miR160, miR167	⇧		Fahlgren *et al.* 2007
	miR825		⇩	
Fungi	miR156, miR159, miR164, miR171, miR396		⇩	Xin *et al.*2010
	miR393, miR444, miR827	⇧		
	miR7696	⇧		Campo *et al.* 2013
Nematode	miR161, miR164, miR167a, miR172c, miR396a,b, miR398a		⇩	Hewezi *et al.* 2008

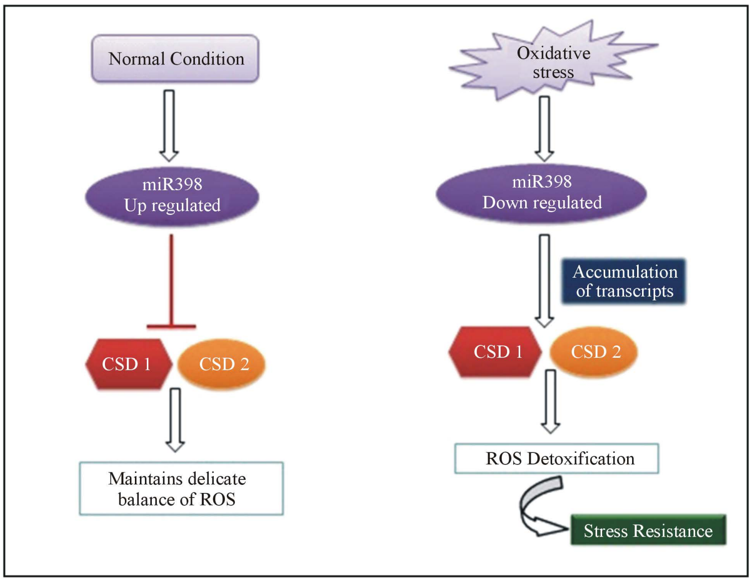

Figure 1. Role of miR398 in Oxidative stress.

accumulation of miR169g is transcriptionally regulated by CBF/DREBs transcription factors [37]. The result of a study of Genome wide profiling on drought-stressed rice found that 16 miRNAs—miR156, miR159, miR168, miR170, miR171, miR172, miR319, miR396, miR397, miR408, miR529, miR896, miR1030, miR1035, miR1050, miR1088, and miR1126 were down regulated and 14 miRNAs—miR159, miR169, miR171, miR319, miR395, miR474, miR845, miR851, miR854, miR896, miR901, miR903, miR1026 and miR1125 were up regulated in response to drought stress [50]. In Populus, miR171l-n, miR1445, miR1446a-e, miR1444a, miR1450, miR482.2, miR530a, miR827, miR1448 and miR1447 were found to be drought-responsive miRNAs [52]. In *P.vulgaris*, miRS1, miR1514a and miR2119 were found to be moderately up regulated whereas miR159.2, miR393 and miR2118 were found to be highly up regulated [46]. In *Medicago truncatula*, miR169 was found to be down regulated only in the roots and miR398 a, b and miR408 was strongly up regulated [53]. In a study on drought-resistant wild emmer wheat (*Triticum turgidumssp. dicoccoides*) 13 differentially regulated miRNAs were reported—miR1867, miR896, miR398, miR528, miR474, miR1450, miR396, miR1881, miR894, miR156, miR1432, miR166 and miR171 [54].

4.3. Salinity Stress

Salinity is the most serious abiotic stress. High salinity interferes with the plants' ability to uptake water causing similar conditions as drought [55]. In rice, three salt-inducible members of the miR169 family—miR169g, miR169n and miR169o and miR393 were found [56] [57] which specifically cleaves the NF-YA gene transcripts. In Arabidopsis, miR156, miR158, miR159, miR165, miR167, miR168, miR169, miR171, miR319, miR393, miR394, miR396 and miR397 were found to be up regulated while miR398 was down regulated [48]. In *P. vulgaris* miRS1 and miR159.2 were found to be highly upregulated [46]. In *P. trichocarpa*, miR530a, miR1445, miR1446a-e, miR1447 and miR171l-n were down regulated whereas miR482.2 and miR1450 were up regulated [16]. A recent microarray experiment on salt-tolerant and salt-sensitive *Zea mays* have identified 98 miRNAs from 27 families, miR156, miR164, miR167 and miR396 families members were reported to be down regulated, while miR162, miR168, miR395 and miR474 families were up regulated in salt-shocked maize roots [58].

4.4. Cold Stress

Studies have found miR319c as a biomarker in response to cold stress. It regulates the mRNA levels of TCP transcription factors [59] while miR397 targets the laccase family members LAC2, LAC4, and LAC17 which are important in the lignification process [60] [61]. The up regulated cold-stress responsive miRNAs—miR393, miR397b, miR402 and miR319c of Arabidopsis were first reported by Sunkar and Zhu in 2004. Many miRNAs were found to be significantly up-regulated—miR165/166, miR169, miR172, miR393, miR396, miR397 and miR408 while other miRNAs—miR156/157, miR159/319, miR164, miR394, miR398 were transiently regulated in response to cold stress [62]. miR397 and miR169 were found to up regulated in Arabidopsis [39] [48], Populus [16] and Brachypodium [63] while miR172 was up regulated in Arabidopsis and Brachypodium. In Populus, miR168 a, b and miR477 a, b were up regulated while miR156g-j, miR475a, b and miR476a were found to be down regulated [16]. In rice, 18 miRNAs—miR156k, miR166k, miR166m, miR167a/b/c, miR168b, miR169e, miR169f, miR169h, miR171a, miR535, miR319a/b, miR1884b, miR444a.1, miR1850, miR1868, miR1320, miR1435 and miR1876 were identified [64].

4.5. UV Radiation

UV radiation causes molecular damage at the DNA, RNA levels along with hyper accumulation of ROS [65]. In a study on Arabidopsis found 21 putative light-responsive miRNAs belonging to 11 different miRNA families—miR156, miR159, miR160, miR165/166, miR167, miR169, miR170, miR172, miR393, miR398 and miR401 [65]. In *Populus tremula*, 24 UV-B stress-responsive miRNAs (13 up-regulated and 11 down-regulated) were identified [66]. The three miRNA families—miR159, miR169, and miR393 were found to be up regulated in Arabidopsis but were down regulated in *P. tremula*, which suggests that UV-B radiation stress response maybe species-specific [66].

4.6. Nutrient Stress

miRNAs are vital in fine-regulation of nutrient homeostasis. According to different studies in Arabidopsis, potential biomarkers in response to nutrient stress such as in phosphate- miR399, sulfate- miR395, and copper-miR398 were reported [3]. miR399 partially controls phosphate equilibrium [3]. Under phosphate deficient condition the PHO2 gene which encodes an E2 ubiquitin conjugase related enzyme (E2-UBC24) is down- regulated and miR399 is up regulated [67]-[69]. The synthesis of miR399 is induced by PHOSPHATE STARVATION RESPONSE (PHR1) transcription factors which bind to GNATATNC cis elements for regulation of the phosphate—responsive genes [70]-[72]. The mature miR399 are synthesized in shoots and then moves via phloem to roots where it cleaves the targeted PHO2 transcripts [73] causing phosphate uptake by upregulating the phosphate transporters Pht1;8 and Pht1;9. As the phosphate balance improves, IPS1 (Induced by Phosphate Starvation) acts as target mimic of miR399 to prevent degradation of PHO2 transcripts. The miR399-PHO2-IPS1 is thus an important cycle for Pi-deficiency signaling pathway in order to maintain phosphate homeostasis [37] (**Figure 2**). miR395 has been found to regulate the expression of low-affinity sulfate transporter AST68 (AtSULTR2;1) which functions in internal translocation of sulfate from roots to shoots and also targets ATP sulfurylases—APS1, APS3 and APS4 which functions in the sulfur assimilation pathway [38] [74]-[76]. Although the mechanism of how miR395 regulates in sulfate homeostasis has not yet been clarified. miR398 plays a vital role in Copper homeostasis. Under Cu-stressed conditions, the miR398 is up-regulated resulting in degradation of CSD1 and CSD2 transcripts to save Cu^{2+} for essential processes [36] [77]. Three conserved miRNA families—miR397, miR408 and miR857 were also found to be up-regulated under copper starvation as they targets transcripts which encodes Cu-containing laccase and plantacyanin [60]. The plantacyanin and LAC3, LAC12 and LAC13 transcripts are found to be targeted by miR408 and miR397 targets mRNAs of LAC2, LAC4 and LAC17 while miR857 targets the LAC7 transcript.

4.7. Heat Stress

Sudden increase in temperature (heat shock) leads to denaturation of proteins (enzymes) and interferes with cellular machineries to repair proteins and membranes. In response to heat stress, differential miRNA expression was observed in wheat. Among the 32 miRNA families found in wheat, nine were conserved heat responsive miRNAs. miR172 was found to be down regulated and other miRNAs—miR156, miR159, miR160, miR166, miR168, miR169, miR393 and miR827 were found to be up regulated in response to heat stress [28].

4.8. Mechanical Stress

miRNAs are regulated by mechanical stress which have functions in the structural and mechanical fitness of plants. In a study conducted on *P. trichocarpa*, it was observed that miR156, miR162, miR164, miR475, miR480 and miR481 were found to be down regulated but miR408 was up regulated. miR160 and miR172 were down regulated only in compressed-stressed tissue whereas miR168 was up regulated in tension-stressed tissues [3] [78].

4.9. Phyto-Hormone-Mediated Stress

Phyto-hormones such as Auxins, Abscisic acid (ABA), Ethylene and Jasmonate all are necessary for plant responses to various abiotic stresses [37]. In Arabidopsis, miR159 was found to regulate the ABA signaling pathway. Under dehydration stress, miR159 are induced by transcription factors Abscisic acid Insensitive—ABI3 and ABI5. The accumulated miR159 cleaves two MYB transcription factors—MYB101 and MYB33 resulting in hyposensitivity to ABA. The desentitization of the hormone signalling helps plants to resume growth [79]. In another study, the AUXIN RESPONSE FACTOR 10 (ARF10) transcription regulator was found to be targeted by miR160 in response to ABA stress during germination [80]. In Arabidopsis, miR160, miR393, miR397b, miR402, miR417 were found to be up regulated whereas miR169 and miR398 were found to be down regulated. In contrast, in rice miR319 was up regulated and miR167 and miR169 was down regulated [39] [80]-[84]. In

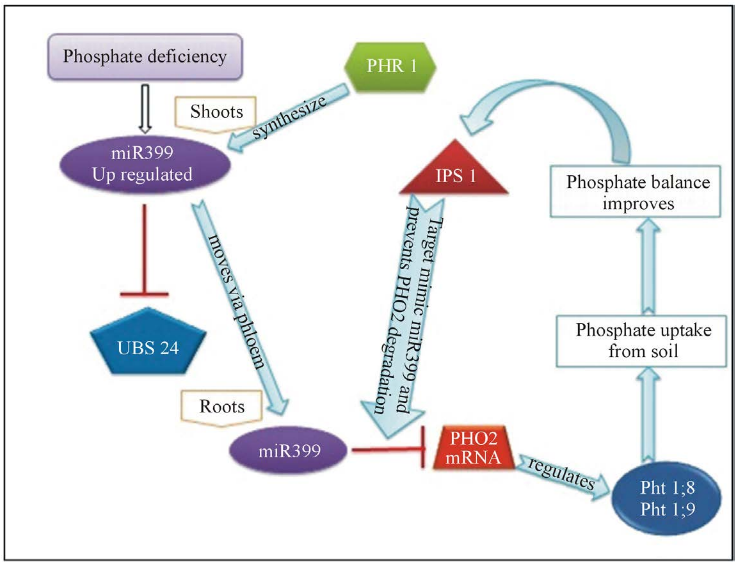

Figure 2. miR399 mediated phosphate homeostasis.

Phaseolus vulgaris, miR159.2, miR393 and miR2118 were induced under ABA treatments whereas miRS1, miR1514 and miR2119 were moderately up regulated in response to ABA [46].

Auxin signaling mediated by miR393 which targets F-box auxin receptor gene- transport inhibitor response1 (TIR1) which proteolysis AUX/IAA proteins by SCF E3 ubiquitin ligases resulting in auxin-induced growth processes. miR393 mediated auxin signaling pathway is linked to biotic as well as abiotic stresses. **Table 2** lists

Table 2. The potential miRNA biomarkers identified in different abiotic stress conditions.

Type of Stress	miRNA biomarkers	Up regulated	Down regulated	References
Oxidative stress	miR398		⇩	Sunkar *et al.* 2006, Yamasaki *et al.* 2007, Jagadeeswaran *et al.* 2009, Kruszka *et al.* 2012
Drought stress	miR393, miR319, miR397	⇧		Sunkar and Zhu 2004
	miR169g, miR171a	⇧		Zhao *et al.* 2007, Jian *et al.* 2010, Zhou *et al.* 2010
	miR156,miR159,miR168, miR170, miR171, miR172, miR319, miR396,miR397, miR408, miR529, miR896, miR1030, miR1035, miR1050, miR1088, miR1126		⇩	Zhou *et al.* 2010
	miR159, miR169, miR171, miR319, miR395, miR474, miR845, miR851, miR854, miR896, miR901, miR903, miR1026, miR1125	⇧		
	miR159.2, miR393, miR2118	⇧		Arenas-Huertero *et al.* 2009
	miR398 a, b, miR408	⇧		Trindade *et al.* 2010
Salinity stress	miR169g, miR169n, miR169o, miR393	⇧		Zhao *et al.* 2009, Gao *et al.* 2011
	miR156, miR158, miR159, miR165, miR167, miR168, miR169, miR171, miR319, miR393, miR394, miR396, miR397	⇧		Liu *et al.* 2008
	miR398		⇩	
Cold stress	miR165/166, miR169, miR172, miR393, miR396, miR397, miR408, miR168a,b and miR477a,b, miR319c	⇧		Zhou *et al.* 2008, Lu *et al.* 2008, Palatnik *et al.* 2007
	miR156g-j, miR475a,b, miR476a		⇩	Lu *et al.* 2008
UV stress	miR159, miR169, miR393	⇧		Jia *et al.* 2009a
	miR156, miR159, miR160, miR165/166, miR167, miR169, miR170, miR172, miR393, miR398, miR401	⇧		Zhou *et al.* 2007b
Phosphate stress	miR399	⇧		Fujii *et al*. 2005, Chiou *et al.* 2006, Bari *et al.* 2006
Copper stress	miR395	⇧		Jones-Rhoades and Bartel 2004, Allen *et al.* 2005, Sunkar *et al.* 2007, Huang *et al.* 2010, Liang and Yu 2010
Sulfate stress	miR398	⇧		Yamasaki *et al.* 2007, Beauclair *et al.* 2010
	miR397, miR408, miR857	⇧		Abdel-Ghany and Pilon 2008
Mechanical stress	miR156, miR162, miR164, miR475, miR480, miR481, miR160, miR172		⇩	Lu *et al.* 2005, Khraiwesh *et al.* 2012
	miR408, miR168	⇧		Lu *et al.* 2005, Khraiwesh *et al.* 2012
Heat stress	miR156, miR159, miR160, miR166, miR168, miR169, miR393, miR827	⇧		Xin *et al.* 2010
	miR172		⇩	

important miRNAs differentially regulated under abiotic stress conditions.

5. Conclusion

Ten years after the discovery of miRNA in *C. elegans*, it was identified in Arabidopsis. Since, then a lot of research has undergone to identify the different miRNAs and their functions. They act as ribo-regulators of gene expression in both plants and animals. The miRBase is the primary repository and database resource for all the published miRNA data. The current release-20 contains 24,521 entries of precursor miRNA in 206 species, which clearly shows the explosive increase in number of miRNA identified in recent times. miRNA are crucial components of stress regulatory networks. The complex trait of plant stress tolerance can be understood by more extensive studies on miRNA-mediated gene regulation. The miRNA profiling of different plant species exposed to the different environmental stresses can help to identify and characterize new miRNA biomarkers. The data obtained from the characterization of the new miRNAs biomarkers and their stress regulatory networks will help in designing tools to improve plant stress resistance or stress tolerance against various stresses. But still most of the miRNA functions are unknown, which creates a large gap between identified miRNAs and their functions. Moreover, the miRNA so far studied for plant stress response has only been limited to some specific plants. So, the current research needs more identification and characterization of plant miRNAs biomarkers from various important plant species.

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