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REVIEW

Orthologous plant microRNAs: microregulators with great potential for improving stress tolerance in plants

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Abstract

Key message **Small RNAs that are highly conserved across many plant species are involved in stress responses.**

Abstract Plants are exposed to many types of unfavorable conditions during their life cycle that result in some degree of stress. Recent studies on microRNAs (miRNAs) have highlighted their great potential as regulators of stress tolerance in plants. One of the possible ways in which plants counter environmental stresses is by altering their gene expression by the action of miRNAs. miRNAs regulate the expression of target genes by hybridizing to their nascent reverse complementary sequences marking them for cleavage in the nucleus or translational repression in the cytoplasm. Some miRNAs have been reported to be key regulators in biotic as well as abiotic stress responses across many species. The present review highlights some of the regulatory roles of orthologous plant miRNAs in response to various types of stress conditions.

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Abbreviations

lsiRNAs	Long-siRNAs
miRNAs	MicroRNAs
nat-siRNAs	Natural antisense siRNAs
rasiRNAs	Repeat-associated siRNAs

Introduction

Plants have the ability of encoding and processing 21–40 nucleotide small RNAs, which can be classified as microRNAs (miRNAs), trans-acting siRNAs (ta-siRNAs), natural antisense siRNAs (nat-siRNAs), repeat-associated siRNAs (rasiRNAs) and 30–40 nt sized long-siRNAs (lsiRNAs; Vaucheret 2006; Jamalkandi and Masoudi-Nejad 2009; Katiyar et al. 2007; Sunkar 2010). Among these, miRNAs are the most abundantly expressed and well-studied class of small RNAs in plants (Jones-Rhoades and Bartel 2004; Voinnet 2009). The miRNAs are small ribonucleic acid molecules found in eukaryotic cells. They are 21–24 nucleotides in length and non-protein coding in nature. The longer, non-protein-coding RNAs that have the ability to form hairpins, act as the precursors for the miRNA molecules (Willmann and Poethig 2007). The miRNAs regulate gene expression at the post-transcriptional stages by targeting mRNAs; this targeting can be either by direct cleavage of mRNAs or indirect by repression of mRNA translation. Consequently, miRNAs may perform important regulatory roles in both plants and animals during organ development, in abiotic and biotic stresses, during phase changes and disease development.

miRNA biogenesis

The biogenesis of miRNAs is a step-wise process. The miRNAs are encoded by MIR genes which are transcribed

by RNA polymerase II into long primary transcripts (pri-miRNAs). The first step in the biogenesis of miRNAs is the synthesis of a large primary transcript. The RNase III enzyme DICER-LIKE1 (DCL1; EC 3.1.26.3) processes pri-miRNA into a hairpin structure called the precursor miRNA (pre-miRNA). This pre-miRNA is folded into a duplex which later forms the mature miRNA along with the complementary fragment, called miRNA*, from the other arm of the precursor (Bartel 2004; He and Hannon 2004). Several proteins such as hyponastic leaves 1 (HYL1), Serrate (SE) and Dawdle (DDL), help the DCL-1 enzyme process the mature miRNA duplex from the hairpin-like structure. To stabilize the duplex a methyl group is added to the 3′ ends of the miRNA duplex by the methyltransferase Hua Enhancer (HEN1). Finally, mature miRNAs are selected from the RNA duplex, and then exported to the cytoplasm by HASTY5 (HST5) (Park et al. 2005; Dezulian et al. 2005). In the cytosol, the duplex is unwound, and the mature miRNA is integrated into Argonaute protein (AGO1), a component of the RNA-induced silencing complexes (RISCs) (Baumberger and Baulcombe 2005; Qi et al. 2005). Since miRNAs and their target sequences show near perfect complementarity, RISC can bind to the target transcripts and regulate gene expression either by causing degradation of target mRNA or by translational repression (Chen 2004; Gandikota et al. 2007; Fig. 1). Recently, Li et al. (2013) showed that the translational inhibition of miRNA occurs in the endoplasmic reticulum. It has also been suggested that Altered Meristem Program1 (AMP1), an integral membrane protein, interacts with AGO1 to facilitate translational inhibition.

Role of miRNA in plant stress

Plants being sessile organisms often have to face stressful conditions and hence they have evolved highly sophisticated mechanisms to cope with such adverse conditions (Sunkar 2010; Kawashima et al. 2011). Plants counter environmental stresses by initiating new growth programs involving minimization of their growth rates and reorganizing their resources (Veselov et al. 2002; Fricke et al. 2006). miRNA analyses via bioinformatics approaches and isolation techniques carried out in the model organism *Arabidopsis thaliana* (L.) first showed that miRNAs are involved in stress response in plants (Rhoades et al. 2002; Sunkar and Zhu 2004).

Abiotic stress involves mild fluctuations over the threshold limits of environmental factors such as light, temperature, nutrients, water availability, carbon dioxide, etc. leading to stressful conditions such as drought, salinity, cold stress, oxidative stress, nutrient deprivation, low oxygen, hypoxia (Sunkar 2010). Plants cope with these stressful conditions primarily by making necessary alterations in the cell cycle, cell division and cell wall constitution. They can also alter metabolism in many ways as well as reprogram the gene expression to accentuate stress tolerance.

Biotic stress caused by many bacteria and fungus also leads to the rapid accumulation of reactive oxygen species (ROS) such as hydrogen peroxide (H_2O_2) and O_2^- (Lamb and Dixon 1997). Studies carried out by various research groups in plants have also shown that small RNAs respond to infection by pathogens such as bacteria, virus, fungus, parasites and insects and hence play an important role in

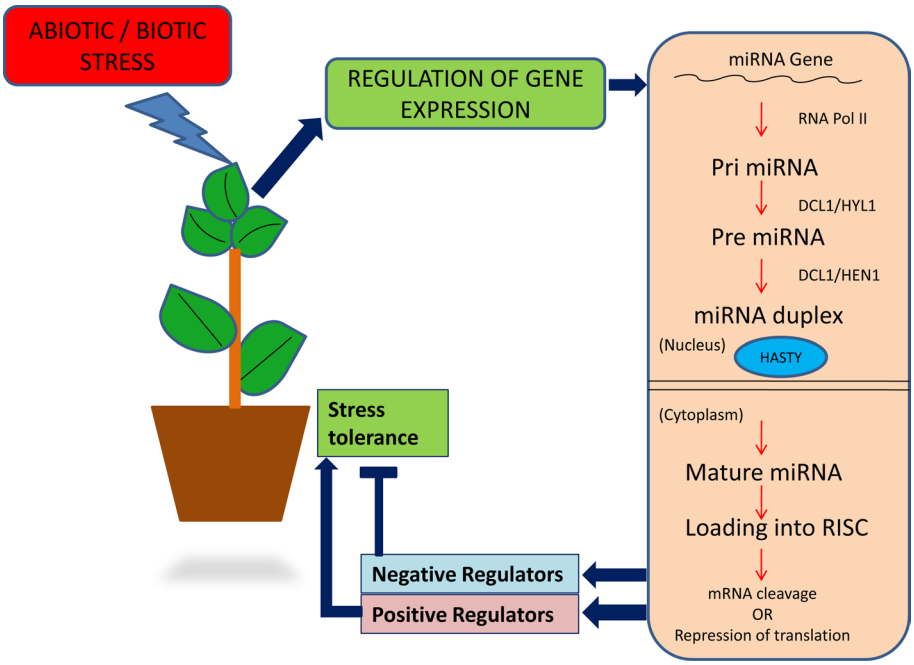

Fig. 1 Regulation of gene expression in plants during stress. In plants, during stress conditions miRNA genes are initially transcribed by RNA Pol II into a single-stranded RNA that folds to form a hairpin structure called Pri-miRNA which is further processed into a Pre-miRNA. With the help of DCL1, a mature duplex miRNA is formed from the hairpin structure which is transported from the nucleus to the cytoplasm by the enzyme HST. Finally mature miRNA is incorporated into the RISC which directs the miRNA to regulate gene expression by either mRNA cleavage or translational repression

plant defense (Navarro et al. 2006; He et al. 2008; Lu et al. 2007).

Micro RNAs for abiotic stress regulation

Plants are frequently exposed to environmental stresses in both natural and agricultural conditions. At the same time, stress also plays an important role in determining distribution of plant species as per soil and climatic conditions. It is noteworthy that some environmental factors such as temperature can become stressful in just a few minutes, while others such as soil water content may take days to weeks and factors such as mineral deficiencies may take months to become stressful. Therefore, it is immensely important to understand the physiological processes that underlie stress injury and the adaptation and acclimatization mechanism of plants to environmental stress. Many micro RNAs have been reported and shown to play crucial roles in regulating abiotic stress tolerance in plants (Fig. 2).

Drought stress

Recent reports have shown that the expressions of miRNAs are fine tuned in response to drought stress. A number of miRNAs have been found to be increased or decreased in abundance during dehydration. In *A. thaliana*, a number of miRNAs namely miR393, miR319 and miR397, miR157, miR167, miR168, miR171, miR408 and miR396 were increased in abundance in response to dehydration while their orthologs miR393 and miR160 g were increased in abundance in *Oryza sativa* L. (Sunkar and Zhu 2004; Zhou et al. 2009; Liu et al. 2008). Similarly, during water stress in *Medicago truncatula*, miR398 and miR408 have been found to be increased in abundance (Trindade et al. 2010). In case of *Populus trichocarpa,* during drought stress the abundance of miR1446a-e, miR1444a, miR1447 and miR1450 were found to be significantly reduced and miR1711a, miR482.2, miR530a, miR827, miR1445 and miR1448 were slightly decreased in abundance (Lu et al. 2008). In *Phaseolus vulgaris* miR2118 was found to be highly induced during drought treatments while miR159.2, miR393 and miR1514 were found to be slightly increased in abundance (Arenas-Huertero et al. 2009). All these studies reported the involvement of various miRNAs in response to drought. In accordance with all those studies it was found that miR393 was consistently increased in abundance during drought stress in most plant species. Drought stress is a major factor that significantly reduces sugarcane yield. In sugarcane like many other plants, miRNAs

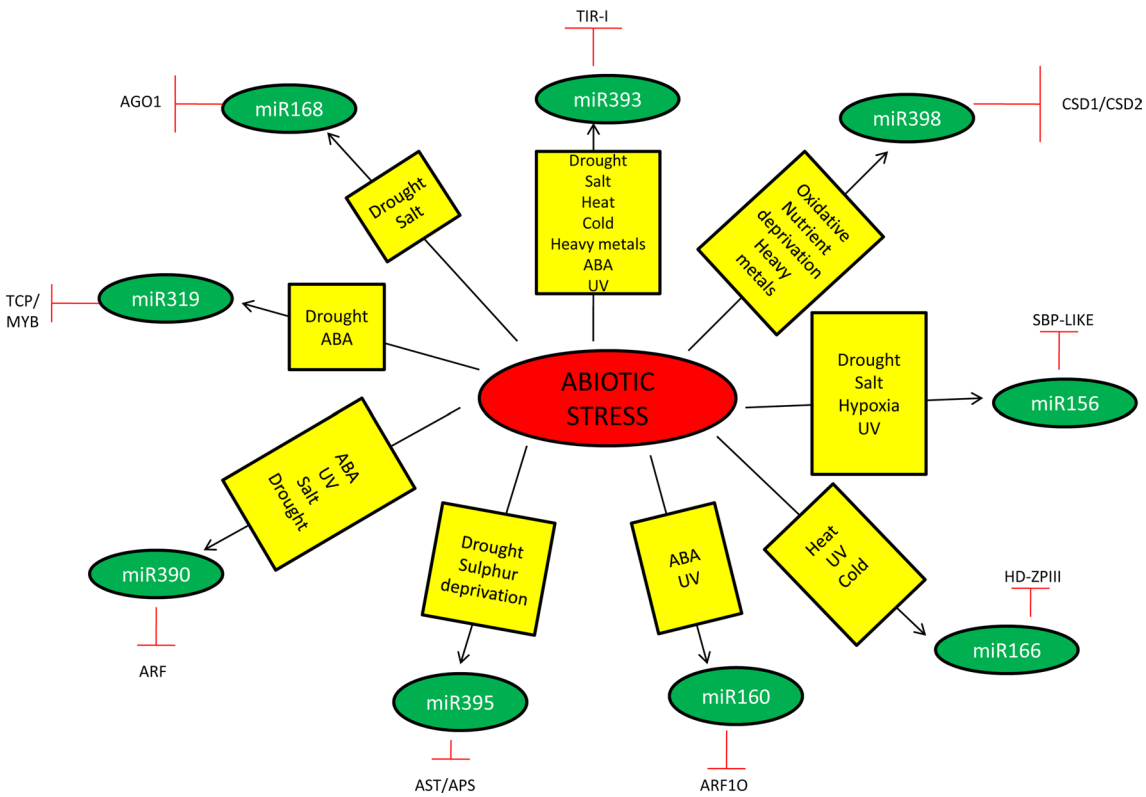

Fig. 2 miRNAs that are increased in abundance during abiotic stress in plants. A display of some common miRNAs those are usually increased during different abiotic stress conditions and their respective targets. *Green ovals* represent increased miRNAs abundance (color figure online)

were found to be involved in stress response. miR393 and miR397 were increased while miR394, miR399 and miR528 were decreased in abundance during drought stress in sugarcane (Ferreira et al. 2012). Studies carried out with respect to leaf growth reprogramming in *Brachypodium distachyon* confirmed the involvement of miR156 and miR167 (Bertolini et al. 2013). Unlike normal conditions where the lateral roots are found to be proliferated, (Chen et al. 2012a, b) found that miR393 is involved in the fine tuning of Transport Inhibitor Response 1 (TIR1) and Auxin Signaling F-Box Protein 2 (AFB2) during hydric stress in *Arabidopsis* resulting in reduction of initiation as well as elongation of lateral roots. High throughput sequencing of drought and salt-treated rice seedlings resulted in identification of 23 novel miRNAs (miR167a, miR810b.2, miR444c.1, miR444c.2, miR444d, miR444e, miR444f, miR1423, miR1425, miR1427, miR1428, miR1429, miR1430, miR1431, miR1432, miR1435, miR1436, miR1437, miR1438, miR1439, miR1440, miR1441, miR1442), all of which were found to be relatively low in abundance (Sunkar et al. 2008). Deep sequencing in potato provided an insight into the involvement of miRNAs in tolerating drought stress. In this regard, it was found that miR811, miR814, miR835, miR1158, miR4398 and miR535 showed decrease in abundance, while miR860 and miR856 showed an increase in abundance (Zhang et al. 2014a, b). Reports on eight drought-responsive long non-coding RNAs in maize showed that seven of them are the precursors of miRNAs namely miR167j, miR169d, miR169h, miR172c, miR399b, miR399e and miR827 (Zhang et al. 2014a, b).

Salt stress

An excessive salt concentration in the soil affects the plant by limiting its water uptake capacity and hence threatens the survival of the plants. Recent studies have also shown and validated the differential regulation of miRNAs during salt stress. In *A. thaliana*, miR156, miR158, miR159, miR165, miR167, miR168, miR169, miR171, miR319, miR393, miR394 and miR396 were shown to be increased in abundance in response to salt stress (Liu et al. 2008). In maize (*Zea mays* L.) microarray was employed to show a number of salt-responsive miRNAs by analyzing the expression pattern of miRNAs in salt-sensitive and salt-tolerant lines. From the study, it was observed that members of miR168, miR162 and miR395 families were increased in abundance while members of miR164, miR167, miR396 and miR150 families were decreased in abundance (Ding et al. 2009). In rice, it was also reported that members of miR169 family namely miR169g and miR169n were induced during salt stress. The miR169 family targets the Nuclear factor Y subunit A (NF-YA) gene by cleaving of the transcription factor that binds to CCAAT box carrying the gene. An ortholog of miR169 was also shown to be increased in abundance in *A. thaliana* during salt stress (Zhou et al. 2007). In *Populus trichocarpa* during salt stress, miR530a, miR1445, miR1446a-e, miR1447 and miR171 l-n were decreased in abundance, whereas miR482.2 and miR1450 were increased in abundance (Lu et al. 2008). A contrasting feature has been observed with respect to miR398 and its target genes CSD1 and CSD2 during salt stress. The decrease in miR398 abundance was followed by the elevated expression of its target genes in *A. thaliana*. Modulation of CSD1 and CSD2 mRNA abundance under stress thus can be thought to be directly dependent on the nature of miR398 response (Jagadeeswaran et al. 2009). Again in *P. tremula* during salt stress the orthologous miRNA has been found to show variable results. Initially the abundance of miR398 increased followed by a steep decrease and then again an increase was observed (Jia et al. 2009). In *P. tomentosa*, miR319, miR393, miR394, miR395, miR398, miR399 and miR408 were observed to increase while miR396 and miR1450 were significantly decreased in abundance during salt stress (Ren et al. 2013). Studies carried out by Dong et al. (2013) in soybean nodules showed the involvement of three novel miRNAs gly_1, gly_3 and miR4416d in the regulation of salt stress responses. Recently, Zhuang et al. (2014) identified six miRNAs (sli-miR156c, sli-miR166i, sli-miR167a, sli-miR397a, sli-miR403a and sli-miR5300) in salt-treated roots of *Solanum linnaeanum* (L.). Of these miR156c, miR166i, miR167a and miR5300 showed a decrease in abundance while miR397a was found to increase in abundance while miR403a showed no change in abundance (Zhuang et al. 2014).

Cold and heat stress

Plant species and even cultivars have different optimum temperature ranges for their proper growth and development. To cope up with the increase and decrease in a temperature which adversely affects their normal growth, plants reprogram their gene expression profiles. A number of miRNAs abundances were reported to be altered in response to cold stress. During cold stress, the abundance of miR165/166, miR169, miR172, miR393, miR396, miR397 and miR408 was significantly increased in *A. thaliana,* while miR156/157, miR159/319, miR164, miR394 and miR398 were only transiently increased (Sunkar and Zhu 2004; Liu et al. 2008). In *P. trichocarpa*, a total of nineteen cold-responsive miRNAs were reported where fifteen of them were increased in abundance and four were decreased in abundance. The miRNAs that were found to be increased in abundance were miR168a,b and miR477a,b while miR156g-j, miR475a,b and miR476a were decreased in abundance (Lu et al. 2008). In *P. trichocarpa* and *B.*

distachyon, miR169 and miR397 were cold up-regulated while miR172 up-regulation was observed in *A. thaliana* and *B. distachyon* (Zhang et al. 2009). Cold-responsive miRNAs were also identified in rice by microarray-based profiling. miRNAs from miR319 and miR167 families were decreased in abundance during the cold treatment (De-Kang et al. 2010). Nine heat-responsive miRNAs were reported in wheat (*Triticum aestivum* L.) by Xin et al. (2010), of which miR172 was shown to be decreased in abundance and miR156, miR159, miR160, miR166, miR168, miR169, miR393 and miR827 were increased in abundance. Deep sequencing analysis in *Brassica rapa* (L.) identified novel miRNAs that were responsive to heat and showed that miR5714 and miR5726 were increased in abundance while miR5716 and miR1885b.3 were decreased in abundance (Yu et al. 2012). Genome-wide identification of cold-responsive miRNAs in *P. tomentosa* reported increases in abundance of pto-miR167c-d, pto-miR167f-g, pto-miR171i-k, pto-miR1450 and pto-miRS11 and decreases in abundance of pto-miR319a-c, pto-miR395b-k and pto-miR169f-I (Chen et al. 2012a, b). Wang et al. (2014) reported that rice overcomes cold stress by partially changing active oxygen scavenging which is a result of down regulation of OsPCF6 and OsTCP21. These two transcription factors are potential targets of *Osa*-miR319b (Wang et al. 2014).

Oxidative stress

Abiotic stresses can increase the production of ROS in metabolically active organelles such as mitochondria, chloroplast in plant cells (Mitler 2002). An increase in ROS can lead to partial or severe oxidation of cellular components leading to oxidative stress. The stress induced ROS is controlled by intrinsic anti-oxidant systems that include enzymatic scavengers which are composed of superoxide dismutases (SODs), peroxidases and catalases. The increase in expression of SOD gene in oxidative stress has been well documented (Jagadeeswaran et al. 2009; Sunkar et al. 2006; Yamasaki et al. 2007; Li et al. 2010a, b). In *A. thaliana* the abundance of Cu–Zn SODs-CSD1, CSD2 transcripts was increased when miR398 abundance decreased which showed that miR398 targets CSD1 and CSD2 (Jagadeeswaran et al. 2009; Sunkar et al. 2006; Yamasaki et al. 2007). A genome-wide analysis of H_2O_2-regulated miRNAs from rice seedlings identified seven miRNAs (miR169, miR397, miR528, miR1425, miR827, miR319a.2, miR408-5p) that are differentially expressed under H_2O_2 treatment that results in oxidative stress. It was observed that miR169, miR397, miR827 and miR1425 were increased in abundance while miR528 was decreased in abundance in the H_2O_2-treated samples (Li et al. 2010a, b).

Hypoxia stress

Hypoxia refers to low oxygen stress which results from certain natural phenomena such as water logging. Hypoxia results in the change of the metabolic switch as well as transcriptome of a plant due to change from aerobic respiration to anaerobic fermentation (Bailey-Serres and Voesenek 2008). Latest studies indicated the involvement of miRNAs in response to hypoxia. Maize seedlings when exposed to submergence during early as well as long-term duration showed differential regulation with respect to miRNAs. miRNAs namely miR167, miR166, miR171 and miR396 were found to be increased in abundance while miR159, miR395, miR474 and miR528 were decreased in abundance during early phase but were increased in abundance after long-term exposure (Zhang et al. 2008). In *A. thaliana* the abundances of miR156g, miR157d, miR158a, miR159a, miR172a,b, miR391 and miR775 increased under hypoxia (Moldovan et al. 2010). In *Z. mays* Liu et al. (2012 confirmed the involvement of miR159, miR164, miR167, miR393, miR408 and miR528 during short-term water logging condition.

Nutrient deprivation

For the normal growth and development of plants an optimal abundance of macronutrients and micronutrients in the soil is required. Excess or insufficiency of any of these nutrients has a negative impact on the plant growth and development (Chiou 2007). The miRNAs can be considered as crucial players in nutrient homeostasis as it has been observed that miR395, miR399, miR398, miR397 and miR408 are increased in abundance when there is a limited supply of specific nutrients (Sunkar et al. 2007; Shukla et al. 2008; Chiou 2007; Burkhead et al. 2009).

Sulfate

Sulfur is an important macronutrient and is available to the plants in the form of sulfate. Sulfate is assimilated in the form of cysteine which has a major role in important metabolic reactions such as protein synthesis and certain compounds that help the plants to survive under stressful conditions (Rausch and Wachter 2005). In *A. thaliana*, it was observed that miR395 was increased in abundance in response to sulfate deprivation (Jones-Rhoades and Bartel 2004). It has been shown that miR395 regulates the expression of low-affinity sulfate transporter SULTR2:1 and the ATP sulfurylases genes ASP1, ASP3 andASP4 which function in the first step of sulfate assimilation (Jones-Rhoades and Bartel 2004; Allen et al. 2005; Sunkar et al. 2007; Huang et al. 2010; Liang and Yu 2010). Various studies regarding miR395 have suggested that the response of

this particular miRNA varies between different plant species. The expression of miR395 was found to be undetectable in *A. thaliana* and *M. truncatula* while it was detected in switchgrass (*Panicum virgatum* L.) grown on optimal concentrations of sulfate (Jones-Rhoades and Bartel 2004; Kawashima et al. 2009; Takahashi et al. 2000). In *B. napus* abundances of miR156, miR160, miR164, miR167, miR168 and miR394 were altered in response to sulfate deprivation (Huang et al. 2010). A study carried out in *A. thaliana* has highlighted the importance of miR395 as an important regulator in sulfate assimilation pathway (Matthewman et al. 2012). During sulfur deficiency the concentration of O-acetylserine, the precursor of cysteine increases which ultimately increases the level of miR395. The transcription factor Sulfur Limitation 1 (SLIM1) also interacts with miR395 and thus increases sulfate assimilation (Kawashima et al. 2011). In addition to the already known targets of miR395 (AST68, APS1, APS3 and APS4), another target At2g28780 was identified. It was also suggested that redox signaling induces miR395 expression during sulfur deprivation in Arabidopsis (Jagadeeswaran et al. 2014).

Phosphorus

Phosphorus is an important mineral element required for the synthesis of nucleic acids and membrane lipids. It has been reported that miR399, miR827 and miR2111 are induced specifically in response to phosphate deprivation (Fujii et al. 2005; Hsieh et al. 2009; Pant et al. 2008; Chiou et al. 2006; Franco-Zorrila et al. 2007). Studies carried out regarding phosphate homeostasis in *A. thaliana* indicated that miR399 was increased in abundance (Fujii et al. 2005; Chiou et al. 2006; Bari et al. 2006). Apart from these, conserved miRNAs such as miR156, miR778, miR169, miR395 and miR398 were also involved under phosphate-deprived conditions (Hsieh et al. 2009). The expression of PHO2/UBC24 (an E2 ubiquitin-conjugating enzyme; EC 6.3.2.19) was negatively regulated by the induced miR399, which then hampers the mobilization of internal phosphate from older to younger leaves. The targets of miR827 and miR2111 were also E3 ligases, which suggest that ubiquitination-mediated protein degradation is commonly employed to cope up the phosphate deprivation (Fujii et al. 2005; Chiou et al. 2006). Studies carried out in soybean indicated the involvement of miRNAs in response to phosphate deficiency. In roots of soybean miR894, miR474 and miR482 were increased in abundance and miR1507, miR894 and miR157 in the leaves were increased in abundance. However, in roots miR168, miR319, miR160, miR396 and miR854 were found to be decreased in abundance (Zeng et al. 2010). Low level of phosphorus in the soil acts as a limiting agent for the production of *Phaseolus vulgaris* L. In this case, miR399 targets *PvPHO2,* which encodes an ubiquitin E2 conjugase that facilitates degradation of P-responsive proteins (Ramirez et al. 2013).

Copper

Copper is an important micronutrient concerned with photosynthesis, respiratory chain and other physiological changes (Chiou 2007). During copper deficiency conditions, miR398 was found to be increased in abundance (Yamasaki et al. 2007). In addition to miR398, miR397, miR408 and miR857 were increased in abundance under low copper conditions (Yamasaki et al. 2007; Burkhead et al. 2009). These miRNAs are known to decrease the abundance of transcripts that code for proteins that contain copper such as Cu/Zn SODs (CSDs; EC 1.15.1.1) and several laccases (EC 1.10.3.2; Yamasaki et al. 2007; Abdel-Ghany and Pilon 2008). The decrease suggested that copper may be saved by the induced miRNA for synthesis of more essential copper-containing proteins such as cytochrome c oxidase (EC 1.9.3.1) and plastocyanin. The miRNAs miR397 and miR408 were shown to be conserved in many plant species including *A. thaliana*, rice and poplar (Jones-Rhoades and Bartel 2004; Sunkar and Zhu 2004; Fahlgren et al. 2006; Bonnet et al. 2004). Studies carried out in common bean supported the importance of miR398b in regulation of copper homeostasis. Nodulin 19 (Nod 19) has been identified as a novel target of miR398b which along with CSD1 participates in ROS detoxification under copper toxicity (Naya et al. 2014).

Boron

Boron deficiency is a major problem in many crop plants. Though it is an established fact that miRNAs play an important role in nutrient starvation but the knowledge relating to the involvement of miRNA in boron deficiency is limited. A recent study carried out in *Citrus sinensis* (L.) roots showed that miR474, miR782, miR834, miR5023, miR394, miR830, miR5266 and miR3465 regulated the adaptation of roots to boron deficiency (Lu et al. 2014).

Heavy metals

Accumulation of heavy metals like cadmium (Cd), chromium (Cr), mercury (Hg), nickel (Ni), lead (Pb) and zinc (Zn) by the plants has become a major global concern as they affect crop productivity and pose a threat to food safety. Cd is a toxic metal when at high concentration results in many physiological and biochemical disorders in plants. Studies related to heavy metals were carried out in *A. thaliana* (Ding and Zhu 2009), rice (Huang et al. 2009), *M. truncatula* (Zhou et al. 2008) and *B. napus* (Huang et al. 2010) which suggested the involvement of miRNAs in

response to heavy metal stress. Zhou et al. (2008) reported that six miRNAs were found to be Cd responsive. miR393, miR171, miR319 and miR529 were increased in abundance while miR166 and miR398 were decreased in abundance. A similar study was carried out in rice by Huang et al. (2009) and a number of miRNAs were found to be responsive to Cd stress. Sixteen miRNAs (miR156, miR159, miR160, miR164, miR166, miR167, miR168, miR169, miR171, miR319, miR393, miR396, miR398, miR529, miR604 and miR806) were found to be involved in Cd stress in rice (Huang et al. 2009). Genome-wide studies were also carried out to identify Cd-responsive miRNAs and their targets in *B. napus*. It was found that miR172f, miR398 and miR857 were increased in abundance while miR159, miR319d, miR394, miR398b and miR2111 were decreased in abundance on Cd exposure in roots. Similarly, on Cd exposure in shoots, miR156 m, miR158, miR158a, miR161, miR400 and miR1885 were increased in abundance whereas miR159, miR162, miR164, miR167f-h, miR167i, miR171, miR319, miR319c, miR349, miR395, miR858 and miR2111 were found to be decreased in abundance (Zhao et al. 2012a). Transcriptome analysis of Cd-treated *Raphanus sativus* roots indicated a total of 22 known and 8 novel miRNAs. miRNAs like miR156, miR159, miR166 and miR319 decreased in abundance while miR398, miR857, miR396a, miR396b increased in abundance (Xu et al. 2013). Zhang et al. (2013) focused on the role of miR395 in detoxification of Cd in *B. napus* and opined that the expression of metal tolerance genes such as *BnPCS1, BnHO1 and Sultr1:1* was increased during Cd stress (Zhang et al. 2013).

Xie et al. (2007) reported the involvement of miR171, miR393 and miR396 on exposure to mercury (Hg) in *B. napus*. Studies carried out in *M. truncatula* report the involvement of miRNAs in response to Hg stress. miR164, miR167, miR172 and miR395 were observed to be increased in abundance whereas miR171, miR390 and miR396 were found to be decreased in abundance (Zhou et al. 2012).

Recent reviews have highlighted the role of several miRNAs in regulating the response of plants toward metal toxicity. Mendoza-Soto et al. (2012) provided an insight into the important regulatory roles of such miRNAs viz. miR319, miR390, miR393 and miR398. The miR319 targets TCP (Teosinte Branched/Cycloidea/PCF) transcription factor thereby playing a role in growth of the plant. miR390 regulates auxin-responsive factors (ARFs) while miR393 represses F-Box auxin receptors TIR1/AFBs and basic helix-loop-helix (bHLH) transcription factors which inhibit auxin signaling. The miR398 targets Cu/Zn superoxide dismutase to control the oxidative stress which results when a plant is exposed to high concentration of iron and copper (Mendoza-Soto et al. 2012). Yang and Chen (2013) reviewed the involvement of several miRNAs (miR159, miR162, miR166, miR171, miR390 and miR396) which decrease in abundance while miR156, miR393 and miR395 increase in abundance on exposure to heavy metals. During heavy metal stress, miRNAs are prone to be increased in abundance by Al and Mn treatments while exposure to As, Cd and Hg depresses the action (Yang and Chen 2013).

UV-B radiation

Depletion of the ozone layer has resulted in an elevated UV-B (280–320 nm) light intensity which has a negative effect on plant growth and development including the generation and accumulation of ROS (Mckenzie et al. 2007). Studies by Zhou et al. (2007) in *A. thaliana* showed that 21 miRNAs were altered on exposure to UV-B radiation. The miRNAs that were increased in abundance under UV-B stress were miR156/157, miR159/319, miR160, miR165/166, miR167, miR169, miR170, miR171, miR172, miR393, miR398 and miR401 (Zhou et al. 2007). In *A. thaliana* and *P. tremula*, miR156, miR160, miR165/166, miR167, miR168 and miR398 were found to be increased in abundance but interestingly miR159, miR169 and miR393 were decreased in abundance (Jia et al. 2009). UV-B responsive miRNAs target a diverse set of genes involved in signal cascade pathways, transcription factors, metabolic pathways and various physiological processes (Lu et al. 2008). The genes encoding the squamosa promoter binding (SPB), a MYB, a NAC domain protein (EC 3.6.5.3), and a homeodomain-leucine zipper protein (HD-ZIP) were predicted to be the targets of miR156, miR159, miR164 and miR165/166, respectively; miR160 and miR167 were predicted to target ARFs (Jia et al. 2009). In wheat, six miRNAs have been reported to be actively involved in regulation after induction by UV-B stress. Of these, three miRNAs miR159, miR167a and miR171 increased in abundance while the three others miR156, miR164 and miR395 decreased in abundance. Moreover, a novel miRNA named Tae-miR6000 has also been isolated from the UV-B treated wheat (Wang et al. 2013).

ABA-mediated stress

Abscisic acid (ABA) is a phytohormone regulating seed maturation and germination, synthesis of seed storage proteins and lipids, stomatal closure, pathogen response and tolerance induction. Studies related to ABA-mediated response were carried out in various plants such as *A. thaliana* (Sunkar and Zhu 2004; Reyes and Chua 2007; Liu et al. 2007; Jung and Kang 2007; Li et al. 2008; Jia et al. 2009), rice (Liu et al. 2009), *P. vulgaris* (Arenas-Huertero et al. 2009) and *Physcomitrella patens* (Khraiwesh et al. 2012). Sunkar and Zhu (2004) reported that miR393, miR397b and miR402 were increased in abundance while miR389a was decreased in abundance by ABA treatment. Reyes and

Chua (2007)-treated germinating *A. thaliana* seeds with ABA and found an increase in the abundance of miR159. Consistent with this, the targets MYB33 and MYB101 transcript abundances were suppressed (Reyes and Chua 2007). Reports have suggested the involvement of miR168 during ABA stress. Both precursor and mature miR168 were found to be induced under ABA stress treatment but it was found that there was no decrease for its target AGO1. It can thus be inferred that transcriptional regulation of miR168 and post-transcriptional control of AGO1 homeostasis may play an important role in ABA stress response (Li et al. 2012a, b). ABA treatment in Arabidopsis regulates the expression of miR394 and its target LCR (Leaf Curling Responsiveness). miR394 silences LCR mRNA which is responsible for maintaining adaptive responses to various abiotic stress conditions (Song et al. 2013).

MicroRNAs for biotic stress regulation

Bacteria, fungi, viruses, nematodes and insects cause immense losses to crop plants. Plants have developed highly sophisticated mechanisms such as gene silencing to fight such epidemics and survive. Recent reports have shown the involvement of miRNAs in modulating biotic stresses and combating such infections (Fig. 3).

Bacterial infection

Plants activate defenses on intrusion of pathogen-associated molecular patterns (PAMPs) such as bacterial flagellin. In *A. thaliana,* Navarro et al. (2006) reported that a flagellin-derived peptide induces miR393. miR393 negatively regulates the expression of AFB1 at transcriptional layer and TIR1, AFB2 and AFB3 at post-transcriptional layer. The increased abundance of miR393 represses auxin signaling which ultimately restricts the growth of *Pseudomonas syringae* (Navarro et al. 2006) (Fig. 4). Recent studies made by Zhang et al. (2011), showed the involvement of miR160, miR167, miR393 and miR159 and their target genes ARFs, i.e., ARF8, ARF10 and ARF16 on *P. syringae* infection. The target genes encode proteins for the biosynthetic or signaling pathways of the auxin, abscisic acid and jasmonic acid (Zhang et al. 2011). It can thus be concluded that the miRNAs play an important role in plant defense by regulating plant hormone pathways. Studies carried out in Cassava highlighted the increase in abundance of miR160, miR167, miR393 and miR390 in response to infection by *Xanthomonas axonopodis* pv. *manihotis*. In the same study, miR535, miR395, miR482, miR397, miR398 and miR408 were found to be decreased in abundance (Perez-Quintero et al. 2012).

Fungal infection

Pathogenic fungi cause severe damage to plants and are important limiting factors for yield and crop quality. miRNAs were shown to mediate changes in gene expression after fungal attack. Twenty-six miRNAs that are responsive to fusiform rust pathogen (*Cornartium quercuum* f. sp. *fusiforme*) were identified from stem xylem of loblolly pine (*Pinus taeda*). It was observed that in galls induced by *C. quercuum*, 10 out of 11 miRNAs families of loblolly pine including 7 pine specific miRNAs were decreased (Lu et al. 2007). In another study, Solexa™ high throughput sequencing was used to isolate 153 miRNAs from wheat leaves infected with the common powdery mildew (*Erysiphe graminis* f.sp. *tritici*) or heat stress. In response to

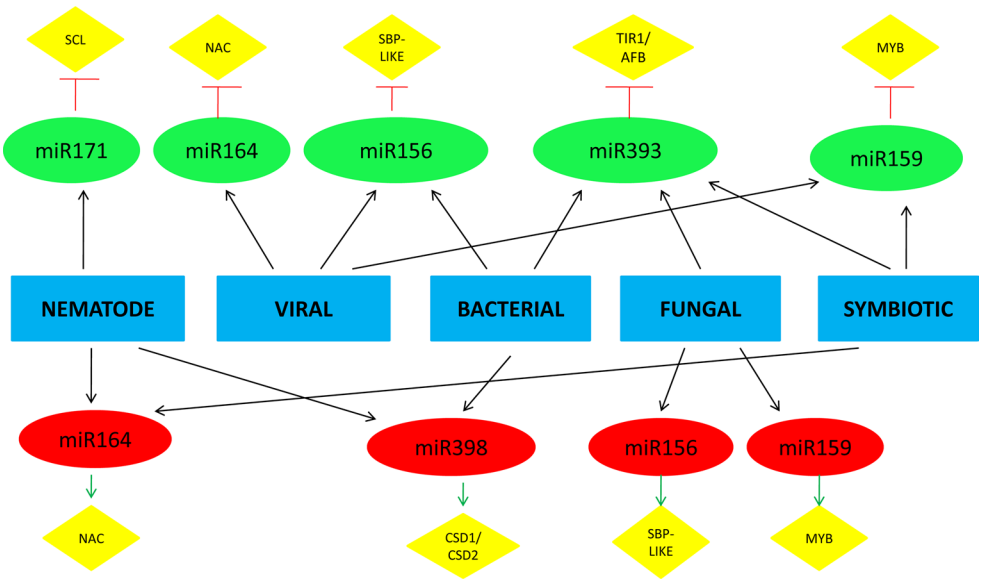

Fig. 3 miRNAs involved in biotic stress response in plants. A depiction of some common miRNAs along with their targets. The miRNAs in *green ovals* represent increased abundances. The miRNAs in *red ovals* represent decreased abundances. The *yellow boxes* represent targets of miRNAs (color figure online)

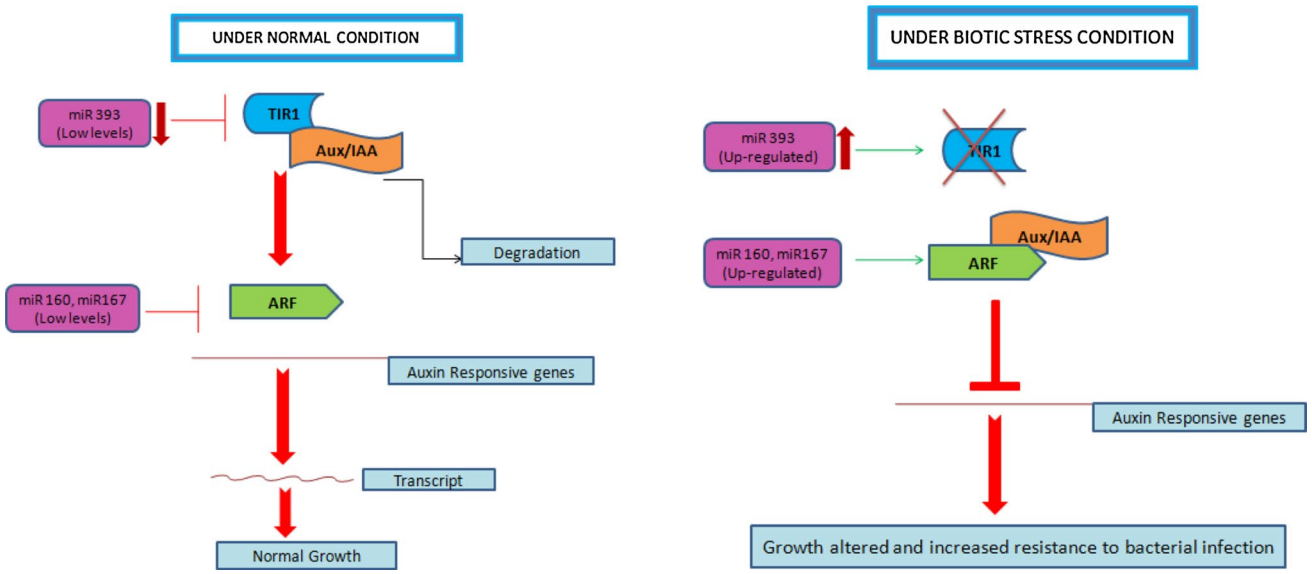

Fig. 4 miRNAs regulate auxin homeostasis under normal and stressful conditions. Expression of auxin-responsive genes that are required for plant growth and development is mediated by the auxin receptor, Transport Inhibitor Response 1 (TIR1). This happens via the release of auxin response actors (ARFs) from auxin/indole acetic acid (Aux/IAA)-mediated heterodimerization. During normal conditions miR393, miR160 and miR167 are present at low abundances which are enough to regulate ARF, required for transcribing auxin-responsive genes. Under stressful conditions, the miR393 abundance is increased which results in the repression of auxin signaling by maintaining low TIR1 and hence increases the heterodimerization of Aux/IAA-ARF. The miR160 and miR167 are also increased during biotic stress, but target ARF and hence decrease its abundance. Repression of auxin signaling restricts bacterial growth thereby suggesting the involvement of auxin in disease susceptibility and miRNA-mediated suppression of auxin signaling in plant resistance

powdery mildew infection in wheat miR156, miR159, miR164 and miR396 were decreased in abundance while miR393, miR444, miR827 were shown to be increased in abundance (Xin et al. 2010; Zhao et al. 2012a, b), reported twelve miRNAs (miR156, miR159, miR160, miR164, miR166, miR168, miR172, miR319, miR398, miR408, miR1448 and miR1450) that increased in abundance in stem bark of *P. trichocarpa* when infected with *Botryosphaeria dothidea* which is involved in the pathological development of stem canker disease. Two novel miRNAs, m0001 and m0002 have been identified in eggplant which might play a role in inducing disease resistance against *Verticillium dahliae* infection. Apart from these, eleven other conserved miRNAs (miR156, miR159, miR160, miR162, miR166, miR167, miR169, miR171, miR172, miR319 and miR396) were slightly decreased in abundance (Yang et al. 2013). Microarray analysis in maize infected with fungus *Exserohilum turcicum* showed that miR811 and miR845 increased in abundance thereby conferring a high tolerance to *Exserohilum turcicum* infection (Wu et al. 2014).

Viral and nematode infection

Viruses are known to cause significant losses to crop plants. It was shown that the abundances of miR156, miR160 and miR164 were increased after viral infection in tobacco (Navarro et al. 2008). In *B. rapa*, infection by *Turnip mosaic virus* (TuMV) increased the accumulation of two new miRNAs, miR159 and miR1885. miR1885 was shown to be more strongly induced than miR159. This increase in the abundance of miRNAs was not observed when *B. rapa* was infected with *Cucumber mosaic virus* (CMV) or *Tobacco mosaic virus* (TMV) (He et al. 2008).

MicroRNAs are also involved in plant–nematode interactions. In response to plant parasitic nematode *Heterodera schachtii* infection, plant miRNAs miR161, miR164, miR167a, miR172c, miR396a,b and miR398a were shown to be decreased in abundance (Bazzini et al. 2007). Deep sequencing techniques also identified 101 miRNAs that were expressed in soybean infected with the Soybean cyst nematode (SCN) (*H. glycines*), which is the most devastating pathogen. The study reported that most of the expressed miRNAs were decreased in abundance and only 6 miRNAs were increased in abundance which inferred that downregulation was important in SCN infection (Li et al. 2012a, b). Two miRNAs have the potential to target the receptor like kinase within the pleiotropic *rhg1/Rfs2* resistance locus (Srour et al. 2012). The miRNAs are miRNA407 and miRNA169a. The latter miRNA family is involved in many different stress responses across many different species.

Table 1 Abiotic/biotic stress regulated miRNAs and their targets: miRNAs are categorized based on their response toward different stress conditions

Stress type	Plant	miRNA	Target	References
ABIOTIC				
Drought	*Arabidopsis thaliana*	miR393 miR 319 miR397	TIR1/AFB TCP/MYB Laccase	Sunkar and Zhu (2004), Chen et al. (2012a, b)
		miR 167 miR 168 miR 171 miR 396 miR408	ARF AGO SCL GRF PCL	Liu et al. (2008)
	Oryza sativa	miR156 miR168 miR172 miR319 miR397 miR408	SPB-LIKE AGO AP2-LIKE TCP Laccase Plastocyanin	Zhou et al. (2010)
		miR393	TIR1/AFB	Zhou et al. (2007)
	Populus trichocarpa	miR1446a-e miR1444a miR1447 miR1450	GRML Polyphenol oxidase Ankyrin repeat L-RTMK	Lu et al. (2008)
	Medicago truncatula	miR398 miR408	CSD PCL	Trindade et al. (2010)
	Phaseolus vulgaris	miR2118	NBS-LRR	Arenas-Huertero et al. (2009)
	Saccharum officinarum	miR393 miR397	AP2-LIKE LACCASE	Ferreira et al. (2012)
		miR394 miR399 miR528	F-Box E2-UBC LRR/F-box	
	Brachypodium distachyon	miR156 miR167	SPB-LIKE ARF	Bertolini et al. (2013)
	Solanum tuberosum	miR811 miR814 miR835 miR4398 miR535	MYB Hydroxyproline-rich glycoprotein Aquaporin WRKY MYB domain-containing protein	Zhang et al. (2014a, b)
		miR860 miR856	Mitogen-activated protein kinase Mitogen-activated protein kinase 19	
Salt	*Arabidopsis thaliana*	miR396 miR168 miR167 miR319/159 miR394 miR156 miR171 miR158 miR169	GRF AGO ARF TCP/MYB F-box SBP-LIKE SCL PPR NFY/MtHAP 2-1	Liu et al. (2008)
	Zea mays	miR167 miR396	ARF GRF	Ding et al. (2009)
		miR168 miR162 miR395	AGO DCL AST/APS	

Table 1 continued

	Populus trichocarpa	miR530a miR1445 miR1446a-e miR1447 miR171	CCHC-type DHPM GRML Ankyrin repeat SCL	Lu et al. (2008)
		miR482.2 miR1450	DRP L-RTMK	
	Populus tomentosa	miR319 miR393 miR394 miR395 miR398 miR399 miR408	TCP AP2-LIKE F-Box AST/APS CSD E2-UBC PCL	Ren et al. (2013)
		miR396 miR1450	GRF Ankyrin repeat L-RTMK	
	Glycine max	gly_1 gly_3 miR4416d	Serine/threonine protein kinase family	Dong et al. (2013)
	Solanum linnaeanum	miR156c miR167a miR5300 miR397a	SPB protein Annexin1 CC-NBS-LRR protein Laccase	Zhuang et al. (2014)
Cold	*Arabidopsis thaliana*	miR165/166 miR169 miR172 miR393 miR396 miR397 miR408	HD-ZIPIII NFY/MtHAP 2-1 AP2-LIKE TIR1/AFB GRF Laccase PCL	Sunkar and Zhu (2004), Liu et al. (2008)
	Populus trichocarpa	miR156g-j miR475a,b miR476a	SBP-LIKE PPR PPR	Lu et al. (2008)
		miR168a,b miR477a,b	AGO GRAS	
	Brachypodium distachyon	miR169 miR397 miR172	NYF Laccase AP2-LIKE	Zhang et al. (2009)
	Oryza sativa	miR319 miR167	TCP ARF	De-Kang et al. (2010)
		miR319b	*OsPCF6* *OsTCP21*	Wang et al. (2014)
	Populus tomentosa	miR167c-d miR167f-g miR171i-k miR1450	ARF ARF SCL Ankyrin repeat L-RTMK	Chen et al. (2012a, b)
		miR319a-c miR395b-k miR169f-l	TCP AST/APS NYF	
Heat	*Triticum aestivum*	miR156 miR159 miR160 miR166 miR168 miR169 miR393 miR827	SBP-LIKE MYB ARF HD-ZIPIII AGO MtHAP2-1 TIR1	Xin et al. (2010)
		miR172	AP2-LIKE	
	Brassica rapa	miR5714 miR5726		Yu et al. (2012)

Table 1 continued

		miR5716 miR1885b		
UV-B radiation	*Arabidopsis thaliana*	miR156 miR159 miR160 miR166 miR167 miR169 miR393 miR398	SBP-LIKE MYB ARF HD-ZIPIII ARF NFY TIR1/AFB CSD	Zhou et al. (2007)
	Populus tremula	miR159 miR169 miR393	MYB NFY/MtHAP2-1 TIR1/AFB	Jia et al. (2009)
		miR156 miR160 miR166 miR167 miR168 miR398	SBP-LIKE ARF HD-ZIPIII ARF AGO CSD	
	Triticum aestivum	miR159 miR167a miR171 miR6000	MYB ARF SCL	Wang et al. (2013)
		miR156 miR164 miR395	SPB-LIKE NAC APS/AST	
Abscisic acid	*Arabidopsis thaliana*	miR159 miR393 miR397 miR402 miR160 miR417 miR319 miR394	MYB TIR1/AFB Laccase HhH-GPD ARF RDRP TCP LCR	(Sunkar and Zhu 2004; Reyes and Chua 2007; Liu et al. 2007; Jung and Kang 2007; Li et al. 2008; Jia et al. 2009; Song et al. 2013)
		miR398a miR169 miR398	Unknown NFY CSD	
	Oryza sativa	miR319	TCP	Liu et al. (2009)
		miR167 miR169	ARF NFY	
Oxidative	*Arabidopsis thaliana*	miR398	CSD1/CSD2	Sunkar et al. (2006)
	Oryza sativa	miR528	LRR/F-box	Li et al. (2010a)
		miR169 miR397 miR827 miR1425	HAP2-LIKE Laccase SPX PPR	
Hypoxia	*Zea mays*	miR159 miR395 miR474 miR528 miR167 miR164 miR393	MYB AST/APS LRR/F-box ARF NAC AP2-LIKE	(Zhang et al. 2008; Liu et al. 2012)
		miR166 miR167 miR171 miR396 miR159 miR408 miR528	HD-ZIPII ARF Spry-2 GRF MYB PCL LRR/F-box	
	Arabidopsis thaliana	miR156g miR157d mir158a mir159a miR172a-b	SPB-LIKE SPL PPR MYB AP2-LIKE	Moldovan et al. (2010)

Table 1 continued

		miR391 miR775	Galactosyltransferase family protein	
Nutrient deprivation				
(a) Phosphorus	*Arabidopsis thaliana*	miR399 miR160	E2-UBC ARF	(Fujii et al. 2005; Chiou et al. 2006; Bari et al. 2006)
	Glycine max	miR894 miR474 miR482 miR1507	PPR R-gene FAMILY	Zeng et al. (2010)
		miR168 miR319 miR160 miR396 miR854	AGO TCP ARF GRF	
	Phaseolus vulgaris	miR399	PHO2	Ramirez et al. (2013)
(b) Sulfur	*Arabidopsis thaliana*	miR395	AST/APS At2g28780	(Jones-Rhoades et al. 2006; Jones-Rhoades and Bartel 2004; Kawashima et al. 2011; Matthewman et al. 2012; Jagadeeswaran et al. 2014)
(c) Copper	*Arabidopsis thaliana*	miR398 miR397 miR408 miR857	CSD and Nod 19 Laccase PCL Laccase	(Naya et al. 2014; Yamasaki et al. 2007; Chiou 2007)
(d) Boron	*Citrus sinensis*	miR782 miR843 miR5023 miR830 miR5266 miR3465 miR394 miR472 miR2118	CCCC-type zinc finger family protein Leucine-rich repeat protein FKBP-type peptidyl-prolyl cis-trans isomerase family protein Ammonium transporter 1:1 Autoinhibited Ca^{2+} -ATPase 11 LCR TIR-NBS-LRR LRR and NB-ARC	Lu et al. (2014)
Heavy metals				
(a) Cadmium	*Medicago truncatula*	miR393 miR171 miR319 miR166 miR398	AP2-LIKE SCL TCP HD-ZIPIII CSD	Zhou et al. (2008)
	Oryza sativa	miR602 miR604	XET WAK-like	Huang et al. (2009)
	Brassica napus	miR164 miR394a-c miR160 miR395	NAC F-box ARF BnPCS1, BnHO1,Sultr1:1	(Huang et al. 2010; Zhang et al. 2013)
	Raphanus sativus	miR156 miR159 miR166 miR396	SPB MYB HD-ZIP TF ARF8	Xu et al. (2013)
(b) Mercury	*Medicago truncatula*	miR395 miR164 miR171 miR390	AST/APS NAC SCL ARF	Zhou et al. (2012)

Table 1 continued

BIOTIC				
Bacterial infection	*Arabidopsis thaliana*	miR156	HD-ZIPII	Navarro et al. (2006)
		miR160 miR167 miR393	ARF TIR1/AFB TIR1/AFB	Zhang et al. (2011)
		miR398	CSD	
	Manihot esculenta	miR160 miR167 miR393 miR390	ARF ARF TIR1/AFB ARF	Perez-Quintero et al. (2012)
		miR535 miR395 miR482 miR397 miR398 miR408	SBP FAMILY AST/APS R-gene FAMILY LACCASE CSD PCL	
Fungal infection	*Pinus taeda*	miR156	SBP-LIKE	Lu et al. (2007)
	Triticum aestivum	miR160 miR156 miR159 miR164 miR171 miR396	ARF SBP-LIKE MYB NAC SCL GRF	Xin et al. (2010)
		miR393	TIR1	
	Solanum melongena	miR156 miR159 miR160 miR162 miR166 miR167 miR169 miR171 miR172 miR319 miR396	SBF-LIKE PPR ARF DCL HD-ZIPIII ARF NFY SCl AP2-LIKE TCP GRF	Yang et al. (2013)
	Zea mays	miR811 miR845	Helix-loop-helix DNA-binding domain-containing protein DNA integration	Wu et al. (2014)
Viral infection	*Brassica rapa*	miR164	NAC	He et al. (2008)
	Nicotiana tobacum	miR1885 miR159 miR156 miR160 miR164	TIR-NBS-LRR PPR SBF-LIKE ARF NAC	Navarro et al. (2008)
Nematode infection	*Arabidopsis thaliana*	miR160 miR164 miR167 miR396 miR398	ARF NAC ARF GRF CSD	Bazzini et al. (2007)
		miR171 siRNA9	SCL At5g18900	
Symbiotic nitrogen fixation	*Glycine max*	miR159 miR166 miR168 miR172 miR393	MYB HD-ZIPII AGO AP2-LIKE TIR1	Subramanian et al. (2008)
		miR160 miR164 miR169 miR396	ARF NAC HAP2-1 GRF	
		miR160	ARF	Turner et al. (2013)

Green: increased miRNAs abundance; Red: decreased miRNAs abundance (color font online)

HD-ZIP Homeodomain-leucine zipper, *AP2* APETELA2, *AGO* ARGONAUTE, *ARF* Auxin response factor, *SPB* Squamosa promoter-binding protein, *CSD* Copper superoxide dismutase, *UBC* Ubiquitin-conjugating enzyme: *TIR1* Transport inhibitor response, *AFB* Auxin F-Box protein, *GRF* Growth-promoting factor, *NFY* Nuclear factor Y, *CCHC* CysCysHisCys-type zinc finger domain, *APS* ATP sulfurylases, *HAP2* transcription factor of CCAAT box-binding family, *SCL* SCARECROW-like protein, *MYB* (myeloblastosis) transcription factor, *PPR* pentatricopeptide repeat proteins, *PCL* Plasma cell leukemia, PHO2: *GRMI* Glutamate receptor metabotropic 1, *NBS-LRR* Nucleotide-binding site-leucine-rich repeat, *DCL* Dicer-like, WAK-like, Cell wall-associated kinases, *LCR* Leaf curling responsiveness

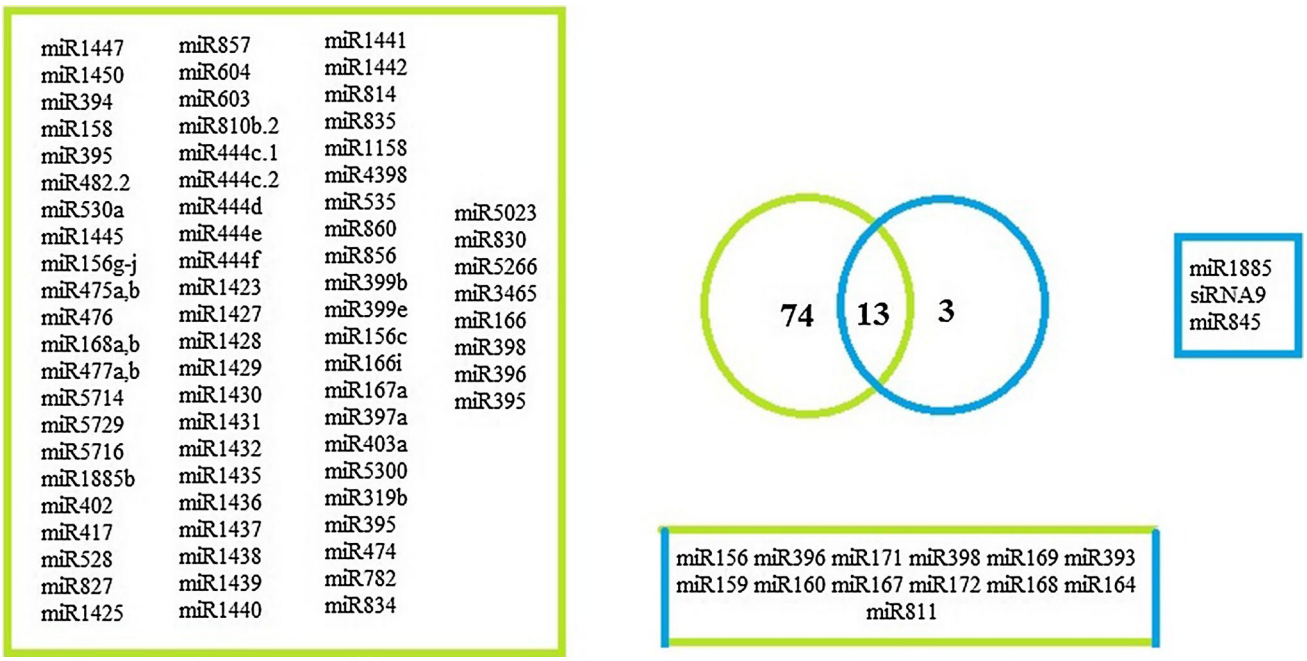

Fig. 5 Venn diagram showing the different miRNAs involved in biotic and abiotic stresses in plants. The *green box* represents miRNAs involved in abiotic stress responses. The *blue box* represents miRNAs involved in biotic stress responses. The *overlapped blue and green box* represents common miRNAs involved both in biotic as well as abiotic stress responses (color figure online)

Symbiotic nitrogen fixation

MicroRNAs have an important and varied role in the process of symbiotic nitrogen fixation in leguminous plants. Differentially expressed miRNAs were identified from the roots of soybean (*Glycine max* L.) which were inoculated with *Bradyrhizobium japonicum,* a symbiotic nitrogen-fixing bacterium. Rhizobial infection decreased the abundance of miR160 and miR169. It was also observed that miR168 and miR172 were increased in abundance at 1 or 3 h post infection (hpi) while miR159 and mi393 were increased in abundance by 3 hpi (Subramanian et al. 2008). The gene expression studies of six families of novel miRNAs and their functions in nodule development in soybean suggested that miR482, miR1512 and miR1515 might have important role in nodulation of soybean (Li et al. 2010a, b). In another study carried out in soybean reported the involvement of miR160 in the inhibition of nodule development (Turner et al. 2013).

Conclusion

An entire new layer of gene regulation has been discovered owing to the advances in identification of miRNAs and siRNAs as components of stress response. The involvement of miRNAs in abiotic as well as biotic stress response has become more clear as a result of sufficient effort channeled toward the studies of stress responses in various crop plants (Table 1). Therefore, a complete understanding of post-transcriptional gene regulation by miRNAs under biotic and abiotic stress will be crucial for understanding and improving stress tolerance in crop plants. Many miRNAs are conserved across species and genus which implies that their biological functions were also conserved. The present review highlighted the role of major orthologous miRNAs that have been found to be involved both in abiotic and biotic stress response where many have been found to be strictly dedicated for a specific type of stress responses (Fig. 5). A detailed understanding of the action of miRNAs depends on the identification of the target genes which also lays the foundation for understanding the complex regulatory networks controlling the physiological as well as developmental processes. There is a need for better understanding of mechanisms governing the coordinated expression of *MIR* genes transcribing various miRNAs to maintain the cellular homeostasis during stress condition in plants. The literature survey here shows that some miRNAs have a major role to play in providing tolerance against biotic and abiotic stress. Since miRNAs are involved in stress tolerance, a better understanding of miRNA-mediated gene regulation can help in designing novel strategies for enhancing various plant traits. The information generated for miRNAs and their targets can be used as a promising tool for improving plant yield, nutritional quality and plant tolerance against various stress conditions.

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Conflict of interest The authors declare that they have no conflict of interest.

Ethical standards The authors declare that the experiments comply with the current laws of the country in which they were performed.

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