



Review

miRNA-mediated regulation of auxin signaling pathway during plant development and stress responses

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Auxin is one of the most important plant growth hormones, playing a crucial role in development as well as in stress responses. Auxin biosynthesis and signaling pathway comprises a series of events including auxin perception by the receptor, activation, and function of auxin response factors and control by auxin repressors. All these factors are regulated by several different microRNAs during leaf, flower and fruit development, anther development, nodulation, lateral and adventitious root development, potato tuber development as well as during heat stress, submergence, boron toxicity, aluminium stress responses, etc., as depicted in the available literature. In this review a thorough study on miRNA-mediated regulation of auxin biosynthesis and signaling has been done in various plant species. The data gathered can be utilized to point out the particular miRNA-mediated regulation module which can be utilized to modulate the expression of the miRNA and thereby modulation of the auxin pathway. Information in this review would be beneficial to utilize the miRNA expression to generate the protocol for engineering plants with altered auxin signaling pathway to obtain better yield and improved stress tolerance.

Keywords. ARF (AUXIN RESPONSE FACTOR); auxin; development; GH3 (Gretchen Hagen3) miRNA; regulation; stress; TIR/AFB (TRANSPORT INHIBITOR RESPONSE 1/AUXIN SIGNALING F-BOX PROTEIN)

1. Introduction

Auxin is one of the most important phytohormone, mainly acting as a regulator of plants growth and development. Also, this hormone may also play significant role in controlling different biotic and abiotic stress responses. Available literature portrays that alteration of genes related to several development as well as stress-related pathways has been found in plants treated with exogenous auxin, indicating their crucial role in regulation of plants' patho-physiological conditions (Ben-Gera *et al.* 2016; Bensmihen 2015; Chae *et al.* 2012; Chen *et al.* 2015; Ding *et al.* 2017). Therefore, precise regulation of auxin biosynthesis and its action is extremely critical for proper growth, development, and fitness of the plant.

miRNAs are short RNA molecules (18–24 nucleotides) crucial in regulating the expression of protein-

coding genes involved in plant development as well as in defense. Almost every pathway in the gene regulation system is directly or indirectly regulated by different miRNAs (An *et al.* 2015; Aravind *et al.* 2017; Armenta-Medina *et al.* 2017; Aukerman and Sakai 2003; Baek *et al.* 2013; Baldrich *et al.* 2014). Like all other mRNAs, miRNAs are also transcribed from endogenous genes called *MIR* gene by mostly RNA polymerase II and rarely RNA polymerase III. The transcript produced from miRNA gene is noncoding in nature and processed to precursors-*MIRNA* and then mature-miRNA via sequential processing steps by the nuclease activity of the enzyme Dicer, a component of miRNA processing machinery (Achkar *et al.* 2016; Chen 2005) (figure 1). This mature miRNA can regulate the expression of other genes with the help of RISC (RNA induced silencing complex) at post transcriptional level via degradation of target transcript and

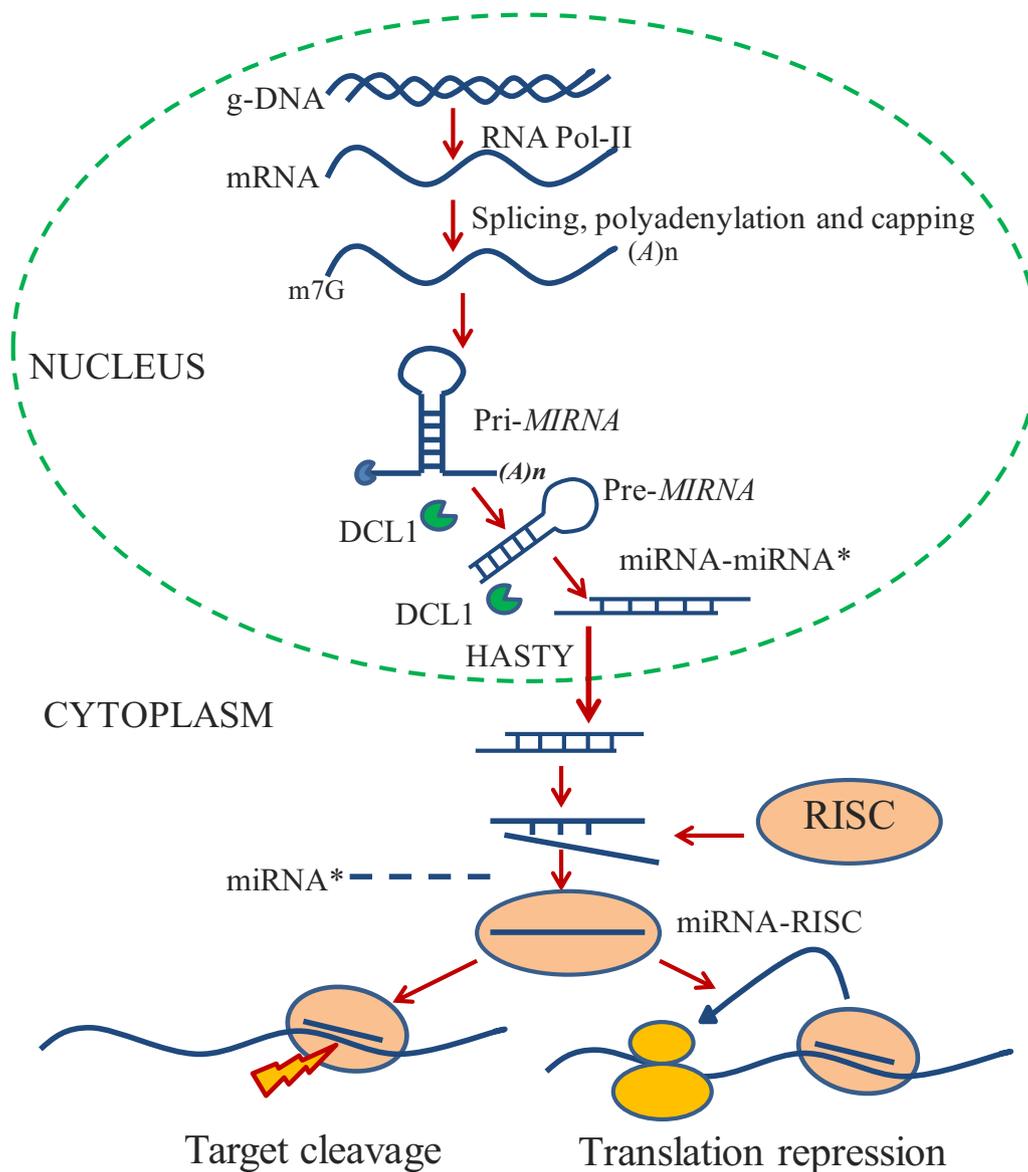


Figure 1. Simplified schematic presentation of the mechanism of biogenesis of microRNA and their function.

translational repression (figure 1). Till date extensive work has been done to understand the regulatory pathways of miRNA (Aukerman and Sakai 2003; Baek *et al.* 2013; Bai *et al.* 2017, Baldrich *et al.* 2014; Damodharan *et al.* 2016; Ding *et al.* 2017; Fang *et al.* 2014; Feng *et al.* 2014; Glazińska *et al.* 2014; Guo *et al.* 2016; Hobecker *et al.* 2017; Huang *et al.* 2016a, b).

Plants possess four different forms of auxin hormone, among them IAA (Indole-3-acetic acid) is the most abundant form. Biosynthesis of auxin and their function is tightly regulated by a complex molecular mechanism involving several different factors with diverse cellular function (Parry *et al.* 2009; Jing *et al.* 2015; Marin *et al.* 2010, Nagpal *et al.* 2005).

Suitable interaction among all the components of that molecular machinery is the sole factor for appropriate auxin signaling (Chen *et al.* 2010; Parry *et al.* 2009; Si-Ammour *et al.* 2011; Smit and Weijers 2015). The signaling pathway is now well characterized, composed of several successive events, each of them crucial for next event to happen accurately. The main three events in the signaling pathway are (i) perception of auxin by receptors, (ii) transport of auxin by transporter and (iii) degradation of repressors by rapid activation of degradation pathway. Three protein families play major role in this whole pathway: Auxin co-receptors TIR1/AFB (F-box TRANSPORT INHIBITOR RESPONSE 1/AUXIN SIGNALING F-BOX PROTEIN), the transcriptional repressors-Aux/IAA (Auxin/INDOLE-3-

ACETIC ACID), and the transcription factors-ARF (AUXIN RESPONSE FACTOR) (Mallory *et al.* 2005; Okushima *et al.* 2005; Parry *et al.* 2009; Salehin *et al.* 2015). ARF proteins function by binding to auxin response elements (AuxRE) present in the promoter of several auxin-regulated genes and regulate their expression (Okushima *et al.* 2005). So far, in *Arabidopsis* 6 TIR1/AFB proteins, 29 Aux/IAA proteins, and 23 ARF proteins have been found (Salehin *et al.* 2015). The function of all these factors depends on the concentration of auxin in the cell. At low auxin levels, the AUX/IAA repressor proteins interact with ARF proteins. Alternatively, at high auxin levels, the auxin binds to TIR1 (component of the SCF ubiquitin ligase complex) which promotes the degradation of AUX/IAA repressor using the 26S proteasome (Jing *et al.* 2015; Parry *et al.* 2009) and thus activates ARF-mediated gene transcription (Alvarez *et al.* 2006; Audran-Delalande *et al.* 2012; Dinesh *et al.* 2016; Fahlgren *et al.* 2006; Glazińska *et al.* 2014; Gutierrez *et al.* 2009; Liu *et al.* 2018; Smit and Weijers 2015; Wang and Guo 2015; Windels *et al.* 2014).

Auxin signaling pathway genes are also found to be the targets of diverse microRNAs. Several microRNAs have been found to be regulated differentially in auxin treated plant. Upregulation in the expression levels of miR398 and miR408b and downregulation of miR156, miR160, miR166, miR167, miR390, miR393, miR482, miR535 and miR2118 has been observed after NAA treatment in Peaches (Shi *et al.* 2017). MicroRNA-mediated regulation of auxin pathway is generally governed by three different lines of attack (i) by regulating the auxin perception by modulating auxin receptors, (ii) by targeting auxin response factors and (iii) by regulating auxin repressors.

Here in this review a thorough study of miRNA-mediated regulation of auxin pathway has been summarized. This review will provide an overall view of miRNA-mediated regulation of auxin signaling pathway and its significance in proper development, stress responses, and other pathways in diverse plant species.

2. Auxin perception is regulated by miRNAs

Auxin signaling pathway is initiated only when auxin is perceived by the auxin receptors present in the surface of the cell. This step is extremely crucial for the commencement of auxin signaling pathway. Inhibitions of auxin perception thus can inhibit this initiation process and completely hamper the downstream signaling. Recent studies have identified certain miRNAs

that can potentially impact this auxin perception by targeting the mRNA of auxin receptor proteins. miR393 has been found to target the auxin receptors, transport inhibitor response-1 (TIR-1) and auxin F-box protein 2 (AFB2), which are the components of the SCFTIR-1 complex and thus negatively regulates auxin signaling pathway by hindering the perception of auxin by the receptors (Chen *et al.* 2015; Guo *et al.* 2016; Windels *et al.* 2014; Wójcik and Gaj 2016). Numerous other literatures have also mentioned the importance of miR393 for proper auxin signaling (Iglesias *et al.* 2014; Si-Ammour *et al.* 2011; Windels *et al.* 2014; Windels and Vazquez 2011). This mode of control mechanism is observed to be very common phenomena during growth, development and stress responses in various plant species (Iglesias *et al.* 2014; Si-Ammour *et al.* 2011). Regulation of seed germination and establishment of rice seedling via miR393-mediated control of auxin pathway has been observed during submergence tolerance in rice (Guo *et al.* 2016; Wójcik and Gaj 2016). In a recent article, Xu *et al.* (2017) have shown that miR393-mediated regulation of TIR1 homologs, regulates fruit/seed set development and leaf morphogenesis in cucumber. The embryogenic transition in *Arabidopsis* has been governed by miR393 via the modification of the tissue sensitivity to auxin treatment (Wójcik and Gaj 2016). Bai *et al.* (2017) have identified two miR393 in barley, and confirmed that HvTIR1 and HvAFB are the target genes by 5'-RACE (rapid amplification of cDNA ends) and degradome data analysis. Further, they have uncovered the fact that miR393/TIR1/AFB module has fundamental role in root development and in aluminium stress response. Rhoades *et al.* (2002) identified another miRNA, miR164 that can potentially target NAC1 transcription factor. This NAC transcription factor can act as an auto-regulatory loop via TIR-1 (Fang *et al.* 2014; Feng *et al.* 2014). Guo *et al.* (2005) found that miR164-directed cleavage of NAC1 mRNA downregulates auxin signals for lateral root development. Lateral root development can also be regulated by the network of miR390, TAS3-derived trans-acting short-interfering RNAs (tasiRNAs) (Marin *et al.* 2010). The small interference RNAs (siRNAs) can target mRNAs encoding ARF2, ARF3 and ARF4. In miR390 overexpression line of *Medicago truncatula*, this miR390/TAS3 regulation promotes the growth of lateral root, whereas the nodulation signaling pathway genes' expression has been downregulated, resulted in decline in rhizobial infection and nodule organogenesis (Hobecker *et al.* 2017). In a recent publication by Santin *et al.* (2017), it has been shown that miR390 can

regulate *Solanum tuberosum* StCDPK1 at the post-transcriptional level and phosphorylates the auxin efflux carrier StPIN4 *in vitro*, a potential downstream target in potato development. Besides development and abiotic stresses miRNA-mediated regulation of auxin signaling plays crucial role in biotic stress response as well. Expression of miR393 has been observed to be upregulated in *Arabidopsis thaliana* plant upon treatment with bacterial peptide flagellin (flg22). In flg22 treated *Arabidopsis*, miR393 targets the auxin receptors F-box TIR1, AFB2 and AFB3, and represses the auxin signaling and thus restricts the growth of *Pseudomonas syringae*. Their data indicates the role of miRNA-mediated regulation of auxin perception in bacterial resistance (Navarro 2016). Sattar *et al.* (2016) have proposed a model for miRNAs impacting auxin perception and auxin-regulated gene expression in response to aphid feeding in *Cucumis melo*.

3. miRNA regulating auxin response factors

Auxin response factors (ARFs) are a family of transcription factors, play an important role in early auxin response (Yang *et al.* 2006; Guilfoyle and Hagen 2007). ARF factors can bind to TGTCTC auxin response elements (AuxREs) found in promoters of early auxin response genes and regulate auxin responsive genes expression (Guilfoyle and Hagen 2007). Several microRNAs have been identified which can target this ARF factors, thereby regulating their downstream auxin responsive genes related to both development and stresses in plant (table 2).

Two microRNA, miR160 and miR167, are found to target three ARFs and regulate their downstream genes' expression to control different developmental pathways in plants. miR160 can target *ARF10*, *ARF16* and *ARF17*. All these three ARFs are transcriptional repressors (Huang *et al.* 2016a; Guilfoyle and Hagen 2007; Liu *et al.* 2016; Mallory *et al.* 2005). ARF10 and ARF16 play an important role in root cap development by restricting stem cell niche and enhancing differentiation of columella cells (Wang *et al.* 2005). Damodharan *et al.* (2016, 2018) have shown the regulation of tomato leaf and flower development, ovary patterning, floral organ abscission and lamina outgrowth is regulated by miR160 via modulation of ARF10-mediated pathway. In *Arabidopsis* miR160-ARF10/ARF16/ARF17 module control somatic embryogenesis (Wójcik *et al.* 2017). *ARF17* can negatively regulate some members of GH3 protein (auxin conjugating enzyme family potentially affecting auxin homeostasis).

miR167 along with AGO1 can repress the function of ARF17 (Mallory *et al.* 2005; Sorin *et al.* 2005). This ARF17 is also the target of miR160. It has been found that plant expressing a modified form of ARF17 which is resistant to miR160-mediated target cleavage, produce higher levels of ARF17 mRNA and have altered accumulation of GH3-like mRNAs associated with numerous dramatic growth defects (Gutierrez *et al.* 2012; Mallory *et al.* 2005). Role of ARF17 in pollen wall pattern formation has been proved by Yang *et al.* (2013), further Wang *et al.* (2017) have shown that miR160-mediated regulation of ARF17 is critical for anther development and pollen formation in *Arabidopsis*. During nodule formation in soybean plant, this miR160 promotes the activity of auxin by targeting ARF10, ARF16 and ARF17 (Nizampatnam *et al.* 2015; Turner *et al.* 2013). In rice miR160 can downregulate ARF18 and thus control the growth and development of rice plant (Huang *et al.* 2016a). miR167 can inhibit the expression of auxin-inducible genes responsible for flower development and lateral root development in *Arabidopsis* and tomato by targeting the transcript of *ARF6* and *ARF8* and IAA-Ala-Resistant 3 genes (Kinoshita *et al.* 2012; Liu *et al.* 2014; Nagpal *et al.* 2005; Wu *et al.* 2006). Gutierrez *et al.* (2009) have shown that the interplay between the function of miR160 and miR167 together regulates the development of adventitious rooting during stress conditions. In this case miR160 targets ARF17 which acts as a positive regulator and miR167 target ARF6 and ARF8 which are the positive regulators of adventitious rooting. In our recent publication we have revealed that miR167a and auxin pathway genes are alternatively regulated during stresses (Jodder *et al.* 2017). It has also been noticed that miR167a precursor and mature forms were regulated at both transcriptional and processing level during various biotic and abiotic stress responses as well as in developmental stages in tomato, indicating their complexity in regulation of target genes expression (Jodder *et al.* 2018).

During lateral root development a feedback regulation of miR390 with ARFs has been observed (Marin *et al.* 2010). Upon upregulation, miR390 triggers the production of TAS3-derived trans-acting short-interfering RNAs (tasiRNAs). These tasi-RNAs negatively regulate the function of ARF2, ARF3 and ARF4. On the other hand, these ARF2, ARF3, and ARF4 influence the accumulation of auxin-induced miR390. This simultaneous positive and negative feedback regulation of miR390 and ARF2, ARF3, and ARF4 regulate lateral root growth by modulating the auxin pathway (Marin *et al.* 2010).

Several reports are now available for the function of ARFs and their miRNA-mediated regulation during abiotic and biotic stress responses. Huang *et al.* (2016b) have shown that miR397a is involved in adaptation to long-term boron toxicity via modulation of secondary cell wall biosynthesis in Citrus. They have confirmed that miR160a and miR397a as the target of four auxin response factor genes and two laccase (LAC) genes respectively during the boron toxicity. Lin *et al.* (2018) proved that during heat stress, expression of miR160 and its precursors are augmented and its targets, ARF10, ARF16, and ARF17 expression is reduced. In *Arabidopsis* plants over-expressing miR160 precursor, seed germination efficiency and survival rate during heat stress is improved. Plant possessing miR160-mimics showed less adaptation efficiency to heat stress. Again in *arf10*, *arf16* and *arf17* mutants presented similar level of heat tolerance to miR160-over expression lines. During biotic stresses also miRNA-mediated regulation of ARFs plays crucial role. Natarajan *et al.* (2018) demonstrate that during *Phytophthora* infection in potato, salicylic acid-mediated systemic acquired resistance (SAR) is regulated by stARF10, target of miR160. Similarly, stARF10 can regulate stGH3.6-mediated crosstalk between salicylic acid and auxin during *Phytophthora* infection. Thus during biotic stress both the local defense response and SAR is regulated by ARF factors. In our publication we have revealed the differential regulation of miR167 and auxin pathway genes during bacterial infections in tomato (Jodder *et al.* 2017).

4. Regulation of auxin repressors by miRNAs

Auxin repressors are also early auxin response genes having role in regulating auxin signaling pathways. Recent studies have found that these repressors may also be the potential target of *MIR* gene products to regulate different physiological events in plant. Wang and Guo (2015) have demonstrated that miR847 can cleave the mRNA of the auxin/indole acetic acid (Aux/IAA) repressor-encoding gene IAA28. Auxin-dependent induction of miR847 positively regulates meristematic competence by cleaving IAA28 mRNA to upregulate auxin signaling, thereby determining the duration of cell proliferation and lateral organ growth in *Arabidopsis*. On the other hand, De Rybel *et al.* (2010) have shown that Aux/IAA repressors IAA28 regulates ARF5, ARF6, ARF7, ARF8, and ARF19 expression, which in turn regulates the expression of GATA23 transcription factor, also of

great consequence for auxin homeostasis during lateral root formation.

5. Conclusion

Inside the cell auxin remains conjugated with different amino acids and carbohydrates. Release of free IAA upon hydrolysis of the conjugate activates the signal transduction pathways. For signaling pathway concentration of auxin is the key determinant. Cytosolic changes in the concentration of auxin are sensed by the receptor and co-receptor includes TIR1/AFB family protein. AUX/IAA family proteins act as transcriptional repressors. The main regulator of IAA is the GH3 proteins. GH3 protein plays vital role in catalyzing the conjugation of IAA with amino acids to maintain free auxin levels in the cell (Bajguz and Piotrowska 2009; Chen *et al.* 2010). These GH3 genes are regulated by different ARFs (ARF8, ARF17 and ARF19) (Mallory *et al.* 2005; Okushima *et al.* 2005; Yang *et al.* 2006) and interestingly these ARFs are the targets of different microRNAs (Li and Zhang 2016; Mallory *et al.* 2005; Sorin *et al.* 2005; Wang and Guo 2015; Yang *et al.* 2006). Our recent publications have shown that GH3, ARFs and miR167 expression is differentially altered during biotic stresses in tomato, indicating miR167 mediated regulation of auxin signaling pathway (Jodder *et al.* 2017). miRNA targeting all different auxin pathway genes and their function in developmental and stress cues in different plant species has been shown in figure 2 and table 1. Tian *et al.* (2004) have shown that in *Arabidopsis* ARF8 regulates the expression of GH3 proteins during lateral root formation and hypocotyle elongation. Available literature depicts that miR167 targets ARF6 and ARF8, and miR160 targets ARF10, ARF16, and ARF17. Different miRNAs, their target sites in the target gene and their predicted mode of action has been summarized in

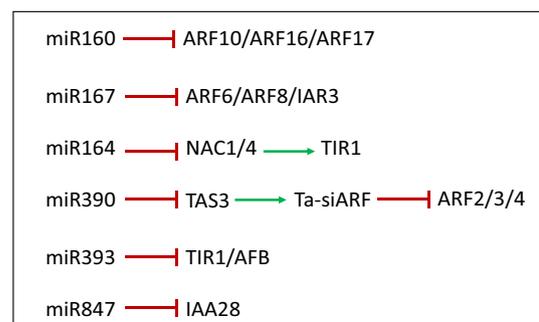


Figure 2. miRNA and their targets regulating auxin signaling.

Table 1. miRNA and their auxin pathway related targets during different development and stress signals in plants

miRNAs	Target genes	Functions	References
miR160	<i>ARF10</i> <i>ARF16</i> <i>ARF17</i> <i>ARF18</i>	Auxin homeostasis Root cap development Boron toxicity Heat tolerance Flower development Pollen wall pattern formation Ovary patterning Floral organ abscission Lamina outgrowth Somatic embryogenesis Systemic acquired resistance (SAR) against <i>phytophthora</i> infection	Rhoades <i>et al.</i> (2002), Jones-Rhoades and Bartel (2004), Wang <i>et al.</i> (2005), Lin <i>et al.</i> (2018), Wójcik <i>et al.</i> (2017), Huang <i>et al.</i> (2016b), Gutierrez <i>et al.</i> (2012), Mallory <i>et al.</i> (2005), Yang <i>et al.</i> (2013), Wang <i>et al.</i> (2017), Nizampatnam <i>et al.</i> (2015), Turner <i>et al.</i> (2013), Huang <i>et al.</i> (2016a)
miR164	<i>NAC1</i>	lateral root development	Fang <i>et al.</i> (2014), Feng <i>et al.</i> (2014), Guo <i>et al.</i> (2005)
miR167	<i>ARF6</i> <i>ARF8</i> <i>ARF17</i> IAA-Ala-resistant 3	Flower development Lateral root development, Adventitious rooting during stress Tolerance to bacterial infections	Jodder <i>et al.</i> (2017), Mallory <i>et al.</i> (2005), Sorin <i>et al.</i> (2005), Kinoshita <i>et al.</i> (2012), Liu <i>et al.</i> (2014), Nagpal <i>et al.</i> (2005), Wu <i>et al.</i> (2006), Gutierrez <i>et al.</i> (2009)
miR390	<i>CDPK1</i> <i>PIN4</i> <i>ARF2</i> , <i>ARF3</i> and <i>ARF4</i> via TasiRNA	Tuber development in potato Lateral root development Control nodule formation	Marin <i>et al.</i> (2010), Hobecker <i>et al.</i> (2017), Santin <i>et al.</i> (2017)
miR393a	<i>TIR-1</i> <i>AFB2</i>	Auxin homeostasis Seed germination Seedling development Fruit/seed set development Leaf morphogenesis Embryogenic transition Root development Aluminium stress response Submergence response	Chen <i>et al.</i> (2015), Guo <i>et al.</i> (2016), Windels <i>et al.</i> (2014), Wójcik and Gaj (2016), Iglesias <i>et al.</i> (2014), Si-Ammour <i>et al.</i> (2011), Windels <i>et al.</i> (2014), Windels and Vazquez (2011), Guo <i>et al.</i> (2016), Wójcik and Gaj (2016), Xu <i>et al.</i> (2017), Bai <i>et al.</i> (2017)
miR397a	laccase (LAC) genes	Secondary cell-wall biosynthesis Adaptation to boron toxicity	Huang <i>et al.</i> (2016b)
miR847	<i>IAA28</i>	Cell Proliferation Lateral Organ Growth	Wang and Guo (2015)

table 2. ARF17 can alter the expression of GH3 during embryonic development as well as in flower and root development (Mallory *et al.* 2005). Therefore, to modulate the expression of GH3, one can modulate the expression of ARFs (ARF8/ARF17) and to modulate the expression of that ARF8 and ARF17, their targeting miRNA miR167 and miR160 expression can be modulated respectively. Using this strategy plants with improved development and stress tolerance can be developed. Transcriptional repressor protein AUX/IAA is also indirectly regulated by miRNA. miR393 targets TIR1 gene family and this TIR protein controls the degradation of Aux/IAA. Therefore, it can be assumed that upregulation of miR393 will affect the degradation of AUX/IAA repressor and thus would probably alter the auxin signaling pathway. The recently discovered

CRISPR/cas9 system can also be utilized to simultaneously modulate the expression of multiple miRNAs to obtain a desired trait for enhanced development or stress responses.

Altogether, available data suggested that miRNA-mediated regulation of auxin homeostasis is a highly conserved process as it has been found in several different species such as *A. thaliana*, *Oryza sativa*, *Solanum lycopersicum*, peaches, and many others (Hendelman *et al.* 2012; Sanan-Mishra *et al.* 2013; Shi *et al.* 2017). miRNA-mediated regulation of auxin pathway is a tightly controlled and complicated process. The efficient action of miRNA can maintain the balance of auxin concentration and signaling for proper growth, development, as well as for combating biotic and abiotic stresses in plant.

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