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MicroRNAs in Control of Plant Development

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In the long evolutionary history, plant has evolved elaborate regulatory network to control functional gene expression for surviving and thriving, such as transcription factor-regulated transcriptional programming. However, plenty of evidences from the past decade studies demonstrate that the 21–24 nucleotides small RNA molecules, majorly microRNAs (miRNAs) play dominant roles in post-transcriptional gene regulation through base pairing with their complementary mRNA targets, especially prefer to target transcription factors in plants. Here, we review current progresses on miRNA-controlled plant development, from miRNA biogenesis dysregulation-caused pleiotropic developmental defects to specific developmental processes, such as SAM regulation, leaf and root system regulation, and plant floral transition. We also summarize some miRNAs that are experimentally proved to greatly affect crop plant productivity and quality. In addition, recent reports show that a single miRNA usually displays multiple regulatory roles, such as organ development, phase transition, and stresses responses. Thus, we infer that miRNA may act as a node molecule to coordinate the balance between plant development and environmental clues, which may shed the light on finding key regulator or regulatory pathway for uncovering the mysterious molecular network.

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The regulation of gene expression is the basis of various biological phenomena, and thus creates our colorful plant kingdom and provides our daily food. Generally, functional protein-coding genes are elaborately controlled by different kinds of tans-acting factors, such as transcription factors. Thus, there is no doubt that there have been plenty of evidences indicating that transcription factors are the major coordinator in plant growth and development, stress responses, and the crosstalk in different signal transduction pathways (Devaiah et al., 2007; Rushton et al., 2010; Xiao et al., 2013; Fan et al., 2014; Li et al., 2014a).

microRNAs (miRNAs), a kind of widespread small endogenous RNAs ranging from 20 to 24 nucleotides in length, are proved to be a crucial regulator in post-transcriptional gene regulation through translational repression and/or guiding degradation of their mRNA targets (Jones-Rhoades et al., 2006; Zhang and Wang, 2015; Xie et al., 2015b). In human genome, over 60% of human protein-coding genes seem to be the regulatory targets of miRNAs (Friedman et al., 2009; Sunkar et al., 2012). Based on the model plant *Arabidopsis* (*Arabidopsis thaliana*) gene annotation data, among 27,416 protein-coding genes are released in TAIR10 (https://www.arabidopsis.org/index.jsp), 1,359 genes are non-coding RNAs (ncRNAs), and the number of mature miRNA is 427. In contrast with the considerable amount of protein-coding mRNAs are regulated by miRNAs in human, it appears that only about 150 mRNAs are the target genes in plant through degradome sequencing and genome analysis (Addo-Quaye et al., 2008; German et al., 2008; Li et al., 2010; Sunkar et al., 2012). Nonetheless, plenty of studies show that plant miRNAs appear to prefer targeting transcription factors, the majority of them exert potent functions in plant various developmental stages (Sunkar et al., 2012; Nova-Franco et al., 2015; Zhang, 2015). Thus, alteration of miRNAs expression level usually results in significant changes in plant growth and development (Chuck et al., 2009; Meng et al., 2010; Rubio-Somoza and Weigel, 2011; Kamthan et al., 2015).

With increasing human population and decreasing fossil energy, food and energy are currently two growing challenges faced by human beings. Over the past decades, intensive studies have advanced our understanding from miRNA biogenesis to biological functions and regulatory mechanisms. Thus, a consensus is forming that miRNA may act as an important target for improving the agronomic characters of food crop, economic crop, and biofuel plant, to benefit the sustainable development of human being (Trumbo et al., 2015; Zhang, 2015). Fundamentally speaking, plant organs are developed from plant pluripotent stem cell. Considering the remarkable influence on plant stem cell regulation of miRNAs, this review begin with the relationship between miRNA biogenesis and development, then we turn to emphasize our current discoveries of miRNA-mediated plant stem cell regulation and subsequent plant tissue derive. Meanwhile, we also highlight the biological roles of miRNAs in crop plants and miRNA-mediated molecular network formation.

Impairment of Key miRNA Biogenesis Genes Cause Pleiotropic Developmental Defects

Mature miRNAs are single-stranded short RNA sequence with 21–24 nucleotides in length that base pair with target mRNAs. Generally, the miRNA biogenesis involves several interdependent steps, including primary miRNAs (pri-miRNAs) transcription, further processing and modification, RNA induced silencing complex (RISC) loading (Fig. 1).

The transcription of plant pri-miRNAs is similar to protein-coding genes, the majority of them are transcribed from their own transcriptional units termed as *MIR* genes, whose genome sequences are usually located at intergenic regions of protein-coding genes and have their own promoter and independent regulatory pattern (Griffiths-Jones et al., 2008; Chen, 2009; Nozawa et al., 2012). In addition, genome wide analysis show that some miRNAs can be produced from intronic or exonic

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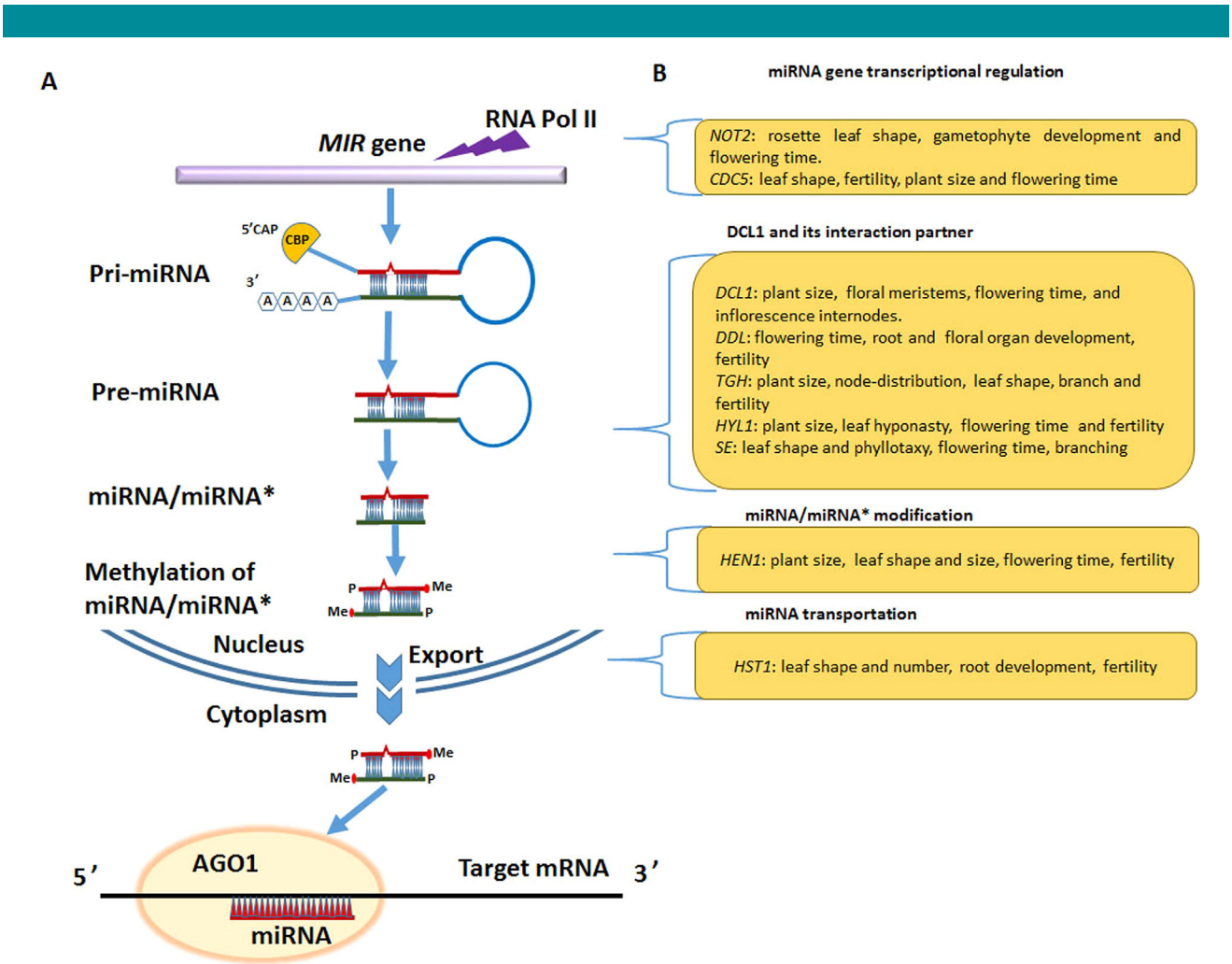

Fig. 1. Misregulation of miRNA biogenesis results in pleiotropic developmental defects. A: A diagrammatic representation of miRNA biogenesis processes. B: Severe developmental impairments result from the mutation of key miRNA biogenesis genes. Negative on TATA less2 (NOT2), CELL DIVISION CYCLE 5 (CDC5), DICER-LIKE1 (DCL1), DAWDLE (DDL), TOUGH (TGH), HYPONASTIC LEAVES1 (HYL1), SERRATE (SE), HUA ENHANCER 1 (HEN1), HASTY 1 (HST1).

regions of protein-coding genes in in rice (*Oryza sativa*) and *Arabidopsis* and share the some cis-regulatory elements with their protein-coding genes (host genes) (Yang et al., 2012b), and even certain miRNAs seem to be encoded by transposable elements (TEs) (Piriyapongsa and Jordan, 2008). In plant, the DNA-dependent transcriptional activator, RNA polymerase II (Pol II), is majorly responsible for transcribing those *MIR* genes to generate large initial transcriptional product referred as primary miRNAs (pri-miRNAs) (Lee et al., 2004). During this step, some auxiliary proteins, such as mediator complex, Negative on TATA less2 (NOT2) protein, elongator complex, assist Pol II to increase its activation (Kim and Chen, 2011; Kim et al., 2011; Wang et al., 2013). Prior to further processing, pri-miRNAs will be capped at their 5′ end and polyadenylated at their 3′ end similar as the most other pol II derived transcriptional event (Chen, 2009). In addition, pri-miRNAs recently show that contain short ORF (open reading frame) sequences involved in the synthesis of regulatory peptides, which can promote the accumulation of their own mature miRNAs (Lauressergues et al., 2015).

In contrast to protein-coding genes, pri-miRNAs harbor an imperfect stem-loop structure, which is need for directing DICER-LIKE1 (DCL1)-mediated cleavage near the base of its stem to generate a precursor miRNA (pre-miRNA) (Park et al., 2002; Chen, 2009). And the pre-miRNA stem-loop structure is further processed by DCL1 into miRNA/miRNA* duplex. For stabilization, the 3′ end of miRNA/miRNA* duplex is methylated by RNA methyltransferase *HUA ENHANCER 1* (*HEN1*) in the nucleus (Kurihara and Watanabe, 2004). In *Arabidopsis*, argonaute protein 1 (AGO1), which possesses endonuclease activity, is the major effector that is responsible for recruiting miRNA to form RISCs (Vaucheret et al., 2004; Baumberger and Baulcombe, 2005; Mallory and Vaucheret, 2006). In this AGO1-centered RISCs, the mature single-stranded miRNA functioned as guides to target complementary mRNAs, while the miRNA* (passenger strand) is often destabilized (Bartel, 2004; Du and Zamore, 2005; Mallory and Vaucheret, 2006; Rogers and Chen, 2013; Bologna and Voinnet, 2014).

Intriguingly, intensive studies indicate that plant miRNAs biogenesis are tightly regulated, otherwise plants would exhibit multiple developmental defects, such as plant size, flowering time, and fertility (Fig. 1), suggesting that miRNAs are the potent regulators in plant development.

miRNAs Play Key Role in Plant Morphogenesis

Just like animal, the various differentiated functional organs are originated from plant stem cells, which are a class of cell population with multiple differentiation potential based on their two distinctive properties, the ability to maintain pluripotent state of themselves and the ability to provide mature specialized cell types (Weigel and Jurgens, 2002). Plant stem cells are confined within specialized niches, shoot apical meristems (SAM), and root apical meristems (RAM), respectively. In higher plants, the formation of shoot meristems generally occurs in two situations, first SAM formation occurs during embryogenesis from the axil of cotyledon(s), and the second SAM formation occurs during post-embryogenesis from the axil of leaves (Fig. 2) (Weigel and Jurgens, 2002; Aida and Tasaka, 2006).

As the critical role of stem cells in plant morphogenesis, meristems studies are always the hot research area. Recent advances are refining our understanding of gene regulation and intercellular signal communication that are represented by miRNA-mediated meristem development.

miRNA-regulated SAM development

Stem cells in the SAM are the precursors of various aerial functional cells and their precise spatio-temporal regulation is the basis of subsequent cell fate determination and organ formation of higher plant (Singh and Bhalla, 2006; Zhang and Zhang, 2012; Zhou et al., 2015). Some miRNAs are proved participate in SAM development, including directly post-transcriptional regulation of key SAM-related genes, act as mobile signal molecules for stem cell maintenance (Zhang and Zhang, 2012; Baumann, 2013; Knauer et al., 2013; Zhou et al., 2015).

The SAM is organized into discrete cell layers, outer cell layer L1 (protoderm), subepidermal layer L2, and inner corpus layer L3 (organizing center, OC), respectively (Satina et al., 1940). WUS (WUSCHEL) protein is a homeodomain transcription factor and its expression in OC cell is essential for maintaining the undifferentiated state of stem cell (Knauer et al., 2013). Base on the key role in SAM development, WUS protein are known to associate with regulation of rice tillers development (shoot branch of rice), the critical factor for rice grain yield (Wang et al., 2014; Tanaka et al., 2015). Previous genetic screen results indicated that *AGO10* (also known as *PINHEAD* and *ZWILLE*), one of nine AGO family members in *Arabidopsis* (Zhang and Zhang, 2012), is key factor of SAM maintenance (Moussian et al., 1998; Lynn et al., 1999; Tucker et al., 2008). Mutation of *AGO10* leads to the failure of embryonic meristem maintenance and exhibit pinhead phenotype (empty apex) in place of the apex (McConnell and Barton, 1995; Moussian et al., 1998; Lynn et al., 1999). And further study demonstrates that *AGO10* appear to participate in the regulation of WUS protein activity and AGO10-mediated SAM maintenance via a non-cell-autonomous mechanism (Tucker et al., 2008). However, AGO10 itself impossible to move between cells and it seems that some signal molecules might implicate in this process (Tucker et al., 2008). Subsequent genetic results show that miR165 and miRNA166, which are very similar and only have one nucleotide difference in mature miRNA sequence (Zhu et al., 2011), display abnormally elevated expression in *ago10* mutant (Liu et al., 2009b). Furthermore, the abnormal shoot-apex phenotypes can be partially rescued by reducing miR165/166 expression in *ago10* mutant plant (Liu et al., 2009b). In addition, miR165/166 are well-characterized that share the same target genes, class *III HOMEODOMAINLEUCINE ZIPPER*

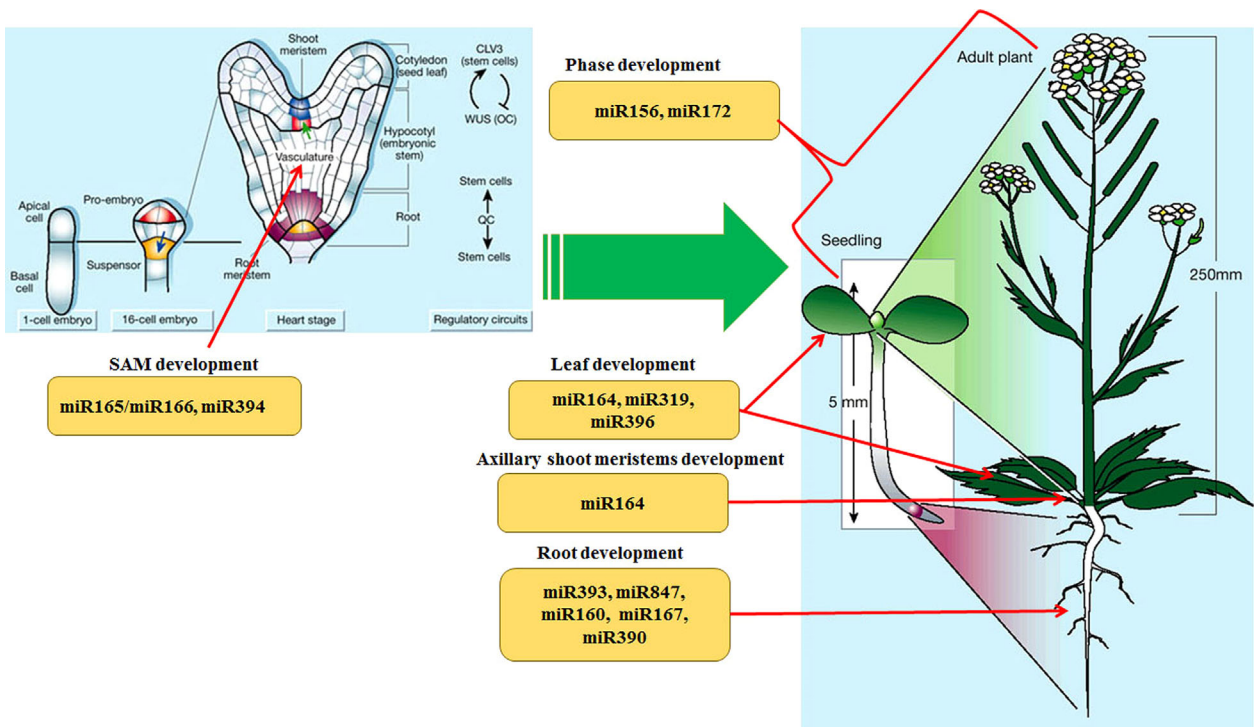

Fig. 2. Schematic model of stem cell-derived plant organogenesis and miRNA-mediated regulation. Images reorganized and reprinted from (Weigel and Jurgens, 2002).

(*HD-ZIP III*) family transcription factors, which mainly involved in SAM-related development, including apical embryo patterning organ, SAM formation and maintenance, and polarity of lateral organs (McConnell et al., 2001; Rhoades et al., 2002; Tang et al., 2003; Prigge et al., 2005; Itoh et al., 2008; Zhu et al., 2011). Therefore, miR165 and miRNA166 are the ideal mobile signal molecules to participate in *AGO10*-mediated non-cell-autonomous regulation, and molecular analysis show that AGO10 can specifically interacts with miR165/166 (Zhu et al., 2011; Zhou et al., 2015). And AGO10 acts just like a decoy for miR165/166 to prevent their repressive function on *HD-ZIP III* genes and maintain the SAM development (Zhu et al., 2011; Zhou et al., 2015).

Similar phenotypes are also observed in maize. *Rolled leaf1* (*Rld1*), a semi-dominant maize mutations, is found that can affect adaxial/abaxial (dorsoventral) polarity of maize leaf (Nelson et al., 2002). Genetic analysis shows that *Rld1* encode a maize *HD-ZIP III* family gene (*rev1*) and share 70% protein sequence identity with *Arabidopsis REV*, one of the five members in *Arabidopsis HD-ZIP III* family genes (Juarez et al., 2004; Zhang and Zhang, 2012). Situ hybridization results show that maize *rev1* gene dominantly express at the tip of SAM and SAM-related regions, which very similar to *Arabidopsis HD-ZIP III* family genes (Juarez et al., 2004). In addition, maize *rev1* also contain the conserved miRNA165/166 complementary site just as it is in *Arabidopsis* (Juarez et al., 2004), suggesting that maize and *Arabidopsis* may share a common regulatory mechanism.

TRANS-ACTING siRNA (ta-siRNAs) is other kind of 21-nucleotide small RNA with same post-transcriptional regulatory functions as miRNAs (Mallory and Bouché, 2008). Genetic results show that ta-siRNAs also functioned in crop plant SAM development, such as maize and rice. For example, *leafbladeless1* (*lbl1*), a recessive mutant of maize, exhibits leaf polarity defects resulting from abnormal development of primordia in meristem (Timmermans et al., 1998). Sequence analysis showed that *LBL1* encodes *SUPPRESSOR OF GENE SILENCING3* (*SGS3*) functioned in the biogenesis of ta-siRNAs (Nogueira et al., 2007). Interestingly, the expression of mir166c, mir166i, and mir166h are activated at the base of the SAM after knocking out of *SGS3* (Nogueira et al., 2007). Consistent with this result, the maize *HD-ZIP III* family genes *rolled leaf2* (*rld2*) in the SAM is dramatically reduced in SGS3 mutant plant (Nogueira et al., 2007). Additionally, the rice *Shoot organization* (*SHO*) gene family and *SHOOTLESS* (*SHL*) gene family are identified as the crucial factor in the initiation and maintenance of SAM (Satoh et al., 1999; Itoh et al., 2000; Satoh et al., 2003). Mutation in those gene loci, including *SHO1*, *SHO2*, and *SHL2*, always causes the complete deletion or impairment of rice SAM (Liu et al., 2007; Nagasaki et al., 2007). On the other hand, *SHO1* encodes DICER-like 4, *SHO2* encodes ARGONAUTE (AGO) 7, and *SHL2* encodes RNA-dependent RNA polymerase 6 (Liu et al., 2007; Nagasaki et al., 2007). All of genes are known to be involved in ta-siRNAs biogenesis pathway (Mallory and Bouché, 2008). Thus, ta-siRNAs are considered that may play important role in SAM formation. However, the abnormal SAM development in *shl* mutant is relate to the rice miR165-*HD-ZIP III* genes regulatory pathway (Nagasaki et al., 2007). Furthermore, the expression of rice *HD-ZIP III* genes, *OSHB1* and *OSHB2*, is dramatically repressed in *sho1* and *sho2* mutant plant, whereas the expression of miR166 increases in *sho* mutant (Nagasaki et al., 2007). Therefore, the synergistic interaction between miRNA and ta-siRNAs may exert conserved functions in SAM maintenance.

In addition to miR165/166-*HD-ZIP III* genes molecular pathway, Laux and coworkers employ ethyl methanesulfonate (EMS) mutants screen system to identify enhancer loci of the weak *ago10-1* stem cell mutant plant and find *enh146* mutant can greatly promote meristem termination in *ago10-1* background (Knauer et al., 2013). Molecular results demonstrate that *ENH146* locus encodes miR394 and repress its expression can impair stem cell maintenance (Knauer et al., 2013). Moreover, the author further shows that miR394 functioned as a mobile signal providing from outer cell layer L1 (protoderm) to maintain stem cell competence in SAM region (Baumann, 2013; Knauer et al., 2013).

miRNA-mediated postembryonic shoot meristem regulation

Embryo-derived shoot meristem (SAM) is mainly responsible for the establishment of main axis and basic body of higher plants and only occurs during embryo development (Fig. 2) (McConnell and Barton, 1998; McSteen and Leyser, 2005; Hibara et al., 2006). In contrast, postembryonic shoot meristem (also referred as axillary shoot meristems) can form in multiple times and is mainly responsible for the initiation of shoot branching and the establishment of inflorescence structures, which are the two key component of crop yield (Komatsu et al., 2003; McSteen and Leyser, 2005; Schmitz and Theres, 2005; Hibara et al., 2006).

Genetic studies prove that tomato (*Solanum lycopersicum*) *Lateral suppressor* (*Ls* or *Las*) gene is the major regulator in axillary meristem initiation, and its mutant plants exhibit severely impairment in axillary bud initiation and inflorescence development (Schumacher et al., 1999). The similar phenotypes also are observed in rice. Rice *MONOCULM 1* (*MOC1*) is identified from spontaneous mutations and show several defects in lateral organ development, including inhibiting the production of shoot branches (tillers), rachis branches, and spikelets (Li et al., 2003). Moreover, *MOC1* share 44% identity to tomato *Las* gene and they are orthologous genes (Li et al., 2003; Schmitz and Theres, 2005). Studies on the *Arabidopsis Las* mutant indicate that *Las* possesses conserved control mechanism in axillary shoot development (Greb et al., 2003). Genetic analysis shows that *Las* appears to act downstream of *CUP-SHAPED COTYLEDON genes1* (*CUC1*) and (*CUC2*), two *Arabidopsis* NAC-domain transcription factors post-transcriptionally regulated by miR164 (Kasschau et al., 2003; Laufs et al., 2004; Hibara et al., 2006). Due to the various developmental defects in *cuc1* and *cuc2* single or double mutant plants, *CUC1* and *CUC2* are suggested to possess several functions, including embryonic meristem initiation, boundary size control and cotyledon establishment (Long et al., 1996; Laufs et al., 2004; Hibara et al., 2006; Raman et al., 2008). Besides, situ hybridization results indicate that *CUC1* and *CUC2* mRNA are accumulated in the axils of leaf primordia and exert crucial role in the establishment of axillary meristems, and miR164-*CUC1*/*CUC2* regulatory mechanism may implicate in the *LAS*-mediated axillary shoot meristems initiation (Hibara et al., 2006; Raman et al., 2008).

miRNAs and leaf development

Plant leaf is the major organ for photosynthesizing and thus plays dominant role in plant biomass and crop plant productivity. The formation of mature leaf involved in several interdependent developmental processes. Firstly, establishment of leaf primordia, which is initiated from undifferentiated cell in SAM peripheral region (Byrne, 2005). During this establishment, it needs the boundary cells to separate leaf primordia from SAM and then differentiate along leaf polarity (Byrne, 2005; Takeda et al., 2011). Thus, the regulator of organ boundaries *CUC1*, *CUC2,* and their controller miR164 have been demonstrated that implicate in leaf development (Rubio-Somoza and Weigel, 2011).

As for crop plant, the sharp and size of leaves are related to the efficiency of photosynthesis and the subsequent yield.

Through activation-tagging approach, a serrated leaves mutant termed *jaw-D* was identified in *Arabidopsis* (Weigel et al., 2000). Interestingly, the insertion site was characterized in intergenic region without open reading frame in it, inferring that *JAW* locus may encode no-coding RNA, this now well-known miR319 (Weigel et al., 2000; Palatnik et al., 2003). To date, several studies suggest that miR319 possesses conserved regulatory function in leaf development. For example, ectopic upregulation of miR319 lead to dramatically changes in the size and shape of tomato leaves (Ori et al., 2007). In addition, overexpression of rice miR319 displays obvious wider leaf blade in rice and creeping bentgrass (*Agrostis stolonifera*) (Yang et al., 2013a; Zhou et al., 2013b).

miR319 mediates the change of plant leaf shape via targeting several TCP transcription factors (Palatnik et al., 2003; Efroni et al., 2008; Schommer et al., 2008). For example, *TCP4* has been identified as the target of miR319 in leaf shape development through screening EMS mutagenesis that attenuate the leaf phenotypes of *jaw-D* plant (Palatnik et al., 2007). Once the EMS-caused mutations dampen the complementary binding of miR319 to *TCP4*, the leaf phenotypes of *jaw-D* plant would be partially recovered (Palatnik et al., 2007). In tomato, *Lanceolate* (*La*) is a partially dominant mutant and change the large compound tomato leaves into small simple ones (Ori et al., 2007). Interestingly, genetic mapping data demonstrate that *La* encodes a TCP transcription factor that contain the complementary sequence for miR319 binding, and the mutation of *La* is happen to occur in the binding site of miR319 and thus interfere the miR319-mediated inhibition (Ori et al., 2007).

Plant *GROWTH-REGULATING FACTORS* (*GRFs*) transcription factors have been reported to implicate in the regulation of leaf growth (Kim et al., 2003). Upregulation of *AtGRF1* and *AtGRF2* give rise to significant enlargement in *Arabidopsis* leaves and cotyledons, whereas triple mutants line of *AtGRF1–AtGRF3* display smaller leaves and cotyledons (Kim et al., 2003). Similar phenotypes also are observed in *AtGRF5* overexpression lines and downregulation lines (Horiguchi et al., 2005). However, miR396 is capable of targeting and post-transcriptional regulating *GRF* genes, and this regulatory interaction between miR396 and *GRFs* exhibits evolutionary conservation among different species. For example, overexpression of *Arabidopsis* miR396a or miR396b results in narrow-leaf phenotypes coupled with repression of six GRF targets, which may through attenuating cell division and proliferation during leaf growth (Liu et al., 2009a; Rodriguez et al., 2010; Wang et al., 2011a). Likewise, the narrow-leaf phenotypes also are found in rice miR396 overexpressing plants (Liu et al., 2014a). In addition to GRF target genes, miR396 can bind some non-conserved bHLH transcription factors. *bHLH74* has been identified as additional target of miR396 in regulating *Arabidopsis* margin and vein pattern formation (Debernardi et al., 2012). Agreeing with this result, the legume *Medicago truncatula* miR396 negatively regulates the expression of not only six *MtGRF* genes but also two bHLH79-like target genes (Bazin et al., 2013).

miRNAs and root system development

As the second party of plant body, plant root system is pivotal for nutrient and water uptake, plant upright, hormone, and secondary metabolites production (Meng et al., 2010). As everyone knows, water and mineral nutrients are two indispensable factors not only for plants surviving and development but also for crop plant environment adaptability and biomass. Thus, the genetic mechanism of plant root system architecture has been intensive studied over the past decades.

Just like SAM, plant root system architecture is also mainly derived from embryonic development and postembryonic development (Rogers and Benfey, 2015). Embryo-derived root architecture comprise plant primary root or/and seminal root, whereas postembryonic development mostly give rise to lateral, crown, and brace root (Rogers and Benfey, 2015). In addition, roots are the belowground organs directly interacting with various environmental factors that can greatly affect the development of plant root system (Bellini et al., 2014). For example, plant always optimizes root system architecture to maximize uptake efficiencies under the condition of drought, phosphorus (P), and nitrogen (N) deficiency (Malamy and Ryan, 2001; Remans et al., 2006; Bayuelo-Jiménez et al., 2011; Hu et al., 2011; Chen et al., 2012; Dai et al., 2012; Bellini et al., 2014Ferdous et al., 2015). Thus, plant root system architecture is result from the coordination between exogenous environmental factors and endogenous signal pathways.

Auxin act as development-related phytohormone and has been proved to be an important modulator of root development (Gutierrez et al., 2012; Orman-Ligeza et al., 2013; Bellini et al., 2014). And recent studies also show that some miRNA play key role in root architecture regulation via post-transcriptional modification of the key auxin signal pathway genes (Wang et al., 2005; Jin et al., 2013; Curaba et al., 2014).

Arabidopsis TRANSPORT INHIBITOR RESPONSE PROTEIN 1 (*TIR1*) is an auxin receptor that directly involves the degradation of *AUXIN/INDOLE ACETIC ACID* (*Aux/IAA*) transcriptional repressors after perceiving auxin signaling (Kepinski and Leyser, 2005; Dharmasiri et al., 2005a). *TIR1* belongs to a small gene family that include five other members *AUXIN SIGNALING F-BOX* (*AFB1-5*), which show distinct biochemical activities and biological roles (Dharmasiri et al., 2005b; Parry et al., 2009). *TIR1* and *AFB2* functioned in the seedling root and are post-transcriptionally negatively regulated by miR393 (Navarro et al., 2006; Parry et al., 2009). OsmiR393a and OsmiR393b are two miRNAs transcribed from rice genome, whose rice overexpression lines show obvious changes in root development involved altered auxin signaling, including primary root elongation and adventitious roots number (Bian et al., 2012). In addition, further results suggest that two rice homologs of *Arabidopsis TIR1*, *OsTIR1* and *OsAFB2*, act as the targets of OsmiR393 (Bian et al., 2012; Xia et al., 2012).

Earlier study has found an IAA/ARF transcriptional repressors *IAA28* involved in *Arabidopsis* lateral root formation and its mutant *iaa28*-1 exhibit severe defect in lateral root initiation (Rogg et al., 2001). Recent research indicates that *IAA28*-regulated lateral root development associates with the *GATA23*, a key transcription factor controlling the specification of lateral root founder cell (De Rybel et al., 2010). In addition, yeast two-hybrid results indicate that IAA28 protein can interact with five ARF proteins (ARF5, ARF6, ARF7, ARF8, and ARF19), which may be essential to auxin-mediated lateral root formation (De Rybel et al., 2010). However, molecular data show that *IAA28* contains partly complementary sequences targeted by miR847 for cleaving (Wang and Guo, 2015). This is further verified by the phenotypical observation that upregulation of miR847 phenocopy the developmental defect in *iaa28*-1 lateral root formation (Wang and Guo, 2015).

Auxin activates its signal transduction and promotes auxin-mediated development mainly via auxin response factor (ARF) family genes (Gray et al., 2001; Zhao, 2010). In *Arabidopsis*, ARF family has 23 members (Remington et al., 2004; Yang et al., 2013b). Among them, *ARF10*, *ARF16*, and *ARF17* can be special targeted by miR160 (Mallory et al., 2005; Yang et al., 2013b). Upregulation of miR160c leads to several changes in root development, such as decrease primary root and increase lateral root number (Wang et al., 2005). More interestingly, the root of *Pro35S:MIR160c* seedings almost lose its gravitropism and exhibit curly primary root, which are the typical phenotypes of root cap defects (Wang et al., 2005). Moreover,

arf10-2 arf16-2 double mutant plants phenocopy *Pro35S:* MIR160c plant in agravitropic root growth (Wang et al., 2005). Thus, miR160 may functioned as a key controller in plant root cap formation thought cleaving *ARF10* and *ARF16* transcripts (Wang et al., 2005). Furthermore, root phenotypic changes also be observed in *Medicago truncatula* and rice miR160 overexpression lines (Meng et al., 2010; Bustos-Sanmamed et al., 2013). However, no obvious differences in root growth rate and lateral root density are found after upregulating the expression of soybean (*Glycine max*) miR160, although miR160 significantly affect the sensitivity to auxin (Turner et al., 2013).

miR167 also be reported to involve in regulating root development by targeting ARF family genes *ARF6* and *ARF8* (Gutierrez et al., 2009). In contrast to the negative regulatory functions of miR160, miR167 exerts positive roles in adventitious root formation (Gutierrez et al., 2009; Gutierrez et al., 2012). Thus, miR160, miR167, and their targets *ARF17*, *ARF6*, and *ARF8* may form a complicated regulatory loop in control adventitious root formation (Gutierrez et al., 2009).

As mentioned above, miRNA sometimes cooperate with the other small RNA molecule such as ta-siRNAs to regulate some biological processes. Another example is that some miRNAs directly mediate the biogenesis of ta-siRNA, such as miR173 responsible for cleaving the transcripts from *TAS1* and *TAS2* loci, miR390 for *TAS3*, and miR828 for *TAS4*, respectively (Axtell et al., 2006; Howell et al., 2007; Montgomery et al., 2008a). Among them, *TAS3* ta-siRNA is capable of targeting and repressing the expression of *ARF2*, *ARF3*, and *ARF4* in regulation of developmental timing and leaf development (Adenot et al., 2006; Fahlgren et al., 2006; Garcia et al., 2006; Hunter et al., 2006; Montgomery et al., 2008b). Interestingly, overexpression of *TAS3* can significantly promote the elongation of lateral roots, combining with expression analysis data that miR390 and *TAS3* have overlapped expression region controlling the lateral root initiation, suggesting that miR390-*TAS3* pathway implicated in lateral root growth (Marin et al., 2010).

In addition, miRNAs are also the major modulator in root-mediated nutrient deficiency and drought responses, which have been reviewed recently (Ferdous et al., 2015; Paul et al., 2015). Thus, miRNAs and their targets may evolve a complicated molecular web to coordinate exogenous environmental clues and endogenous developmental regulation.

miRNAs and Plant Floral Transition

With the growth and development of leaves and root, the adult plant organs have been formed and then will undergo the transition from vegetative to reproductive phase, namely plant floral transition. The successful floral transition is related not only to the plant thriving but also to crop plant productivity. Up to now, there are five flowering time pathways established through studying the annual model plant *Arabidopsis*, including Gibberellic acid (GA) pathway, autonomous pathway, age pathway, photoperiod, and vernalization pathway (Wang, 2014). These pathways together form an elaborate molecular network transducing endogenous and environmental flowering time cues to many floral integrative regulators, such as *SUPPRESSOR OF OVEREXPRESSION OF CO1* (*SOC1*), *FLOWERING LOCUS T* (*FT*), *LEAFY* (*LFY*), and *PETALA1* (*AP1*) (Komeda, 2004). miR156 and miR172 are well-studied miRNAs involved in floral control. As their conserved roles discovered across monocotyledons and dicotyledons, a common view was formed that miRNA may act as potent breeding tool in crop plant genetic improvement.

miR156 and miR172 are two both independent and interrelated miRNA. In expression patterns and regulatory functions, miR172 and miR156 always display some degree of opposite correlation. miR172 expression is hardly detected in plant juvenile phase and accumulating with the developmental time. And overexpressing miR172 promote the flowering time in both monocotyledons and dicotyledons (Zhu and Helliwell, 2010). In contrast, the expression level of miR156 gradually decreases from seeding stage to adult stage, and upregulation of miR156 results in delayed floral transition. In their target genes, the mature 21-nucleotides miR172 binds to the 3′ end near the coding region of AP2 domain transcription factors (Park et al., 2002; Chen, 2004). AP2 transcription factors family exists specifically in plant kingdom and several of their members usually exert repressive roles in flowering time, including *SCHLAFMUTZE* (*SMZ*), SCHNARCHZAPFEN (*SNZ*), *TARGET OF EAT1* (*TOE1*), and *TOE2* (Aukerman and Sakai, 2003; Schmid et al., 2003). However, miR156 is reported to specially target *SQUAMOSA PROMOTER BINDING LIKEs* (*SPLs*) family genes, such as *SPL3* and *SPL9* (Cardon et al., 1999; Rhoades et al., 2002; Xing et al., 2010). And interestingly, many miR156 targets, including *SPL9*, *SPL10*, seems redundantly implicated in the transcriptional regulation of miR172 through binding its promotor region (Wu et al., 2009). Thus, miR156 may act upstream of miR172 and they work together to form a molecular network to control the developmental processes (Wu et al., 2009).

Given the time-related expression pattern and critical regulatory role in plant juvenile-to-adult phase transition, miR156 and miR172 are considered as two main participator in plant age-dependent floral pathway (Bergonzi and Albani, 2011; Wang, 2014). In addition, miR156 and miR172 appear to mediate the interplays between age pathway and other floral pathways. Vernalization refers to many winter ecotypes plants require a certain period of cold treatment to ensure normal flowering time. However, two *Arabidopsis* perennial relative *Arabis alpine* (*A. alpina*) and *Cardamine flexuosa* (*C. flexuosa*) only response this induction when it is at least 5 weeks old (Wang et al., 2011b). It is seem that those perennial plants need some time to develop adult vegetative organs before transferring to reproductive phase. Uncovering the regulatory mechanism and finding that miR156 and miR172 are essential to this kind of age-dependent vernalization behavior, although their subsequent molecular regulations have some differences (Bergonzi et al., 2013; Zhou et al., 2013a). GA is a floral activator and exerts this role through destabilization of several GA repressors DELLA proteins in *Arabidopsis* (Harberd et al., 2009). Molecular data show that the DELLA protein RGA can physically bind to SPL9 and attenuate its transcriptional activities on miR172, *SOC1*, and *FRUITFULL* (*FUL*) (Yu et al., 2012). In photoperiod pathway, *GIGANTEA* (*GI*) is key regulator that mediates photoperiodic flowering by promoting the transcription of *CONSTANS* (*CO*), the core component that is responsible for measuring the distinction of day length (Fowler et al., 1999; Park et al., 1999). However, a report suggests that *GI* also employ the other miR172-dependent pathway in photoperiodic induction, which is independent to *CO* but require the functional *FT*, the target of *CO* (Jung et al., 2007). Moreover, many miR156-targeted SPL genes are able to respond to the photoperiodic changes (Wang, 2014). Thus, miR156 and miR172 are two important members in plant floral signal network, combining their conserved molecular role across monocotyledons and dicotyledons, indicating that those miRNAs may play a bigger role in improving crop productivity.

miRNAs Regulate Key Agronomic Traits of Crop Plant

miRNA and cotton fiber

Cotton is one of the most important economical crops, which produce the natural and renewable textile fiber and its worldwide economic impact is almost US$500 billion annually (Chen and Guan, 2011; Guan et al., 2014b). *G. hirsutum* and *G. barbadense* are two widely cultivated cotton cultivars which account for 90% and 5–8% cotton fiber production of the

world, respectively (Qin and Zhu, 2011). Both of them are allotetraploids and contain two sets of subgenomes, "A" and "D," which diverged approximately 5–10 Myr (million years) ago (Senchina et al., 2003). A-genome diploids species are usually capable of producing shorter cotton fiber and have been used as cultivars in some area, whereas most D-genome diploids species only produce rudimentary fiber that is no useful for textile industry. As the result of the hybridization and polyploidization events occurred in around 1–2 Myr ago (Paterson et al., 2012), those two subgenomes reunited and formed the original wild relatives, which then undergo a long period of domestication and human selection to make sure they can produce agronomically desirable cotton fiber traits. Thus, the emergence of modern spinnable fiber is the process of both natural and human selection.

Through genome sequencing research, many conserved and new miRNAs show that express specifically in *G. hirsutum* fibers and most of their targets may implicate in cotton fiber development (Paterson et al., 2012). Furthermore, miRNAs may form a complicated regulatory network to coordinate different fiber development stages, including initiation, elongation, and secondary cell wall biosynthesis (Liu et al., 2014b; Xie et al., 2015a). Polyploidy is a very common event during plant genome evolution and always confers significant influences in plant productivity and quality, such as tetraploid cottons usually produce better fiber than diploid cottons' (Jiang et al., 1998). In addition, genome analysis demonstrates that cotton A subgenome is considered as the major contributor to fiber improvement, whereas D subgenome is mainly to stress tolerance (Zhang et al., 2015). And miRNAs derived from A subgenome appear to participate in several ovule- and fiber-related biological processes (Xie and Zhang, 2015).

Cotton fiber is a kind of special single-celled trichomes initiated from the epidermal layer of cotton ovule and shares some similar regulatory mechanisms with leaf trichome development (Wan et al., 2014). The *Arabidopsis* R2R3 MYB-domain transcription factor *GLABROUS1* (*GL1*) is key positive controller of trichome initiation (Larkin et al., 1993), and overexpression of a cotton GL1-like MYB transcription factor (referred as *GaMYB2*) can rescue the trichomeless phenotype of *gl1* mutant (Wang et al., 2004). More interestingly, knocking-down the expression of cotton *GhMYB25-like* gene lead to fiberless phenotype but no effect on cotton other trichome formation (Walford et al., 2011). To date, many lines of evidences indicate that MYB family transcription factors are the critical regulator in cotton fiber development (Paterson et al., 2012; Li et al., 2014b, 2015). Among those MYB transcription factors, some of them are predicted to act as the targets of miRNA, such as miR159, miR858, and miR828 (Pang et al., 2009; Guan et al., 2014a). MiR828 and miR858 were recently experimentally proved to coordinate cotton *GhMYB2*-medited *Arabidopsis* trichome and cotton fiber development (Guan et al., 2014a).

Thus, uncovering the underlying regulatory mechanisms underlying miRNA-mediated MYB transcription factors is fundamentally important for understanding cotton fiber formation and subsequent genetic improvement.

OsmiR397 and rice yield

Through genome-wide identification and screening, OsmiR397 was found to highly abundance in rice seeds (Chen et al., 2011; Zhang et al., 2013). After overexpressing its two isoforms, OsmiR397a and OsmiR397b, the author observed that overexpressing rice plants show strongly nodding panicles compared with wild type plants (Zhang et al., 2013). Statistical data demonstrate that overexpression of OsmiR397a and OsmiR397b lead to 7.4 and 13.4% increase in 1,000-grain weight, coupling with the promotion in grain size, including grain length, width, and thickness (Zhang et al., 2013). In addition, OsmiR397 appears to implicate in the regulation of several key yield-related factors, such as vascular bundle formation, panicle branches numbers, effective grains and tiller numbers, grain hull, and endosperm size, which may contribute to the grain yield increased by 17.0%/24.9% in miR397a/b upregulating plants (Zhang et al., 2013). Further molecular and genetic results suggest that miR397-caused grain yield increase result from downregulation of its target gene, rice *laccase* (*LAC*), a regulator involved in brassinosteroids signaling (Zhang et al., 2013). Additionally, the regulatory interaction between miR397 and *LAC* mRNA has been predicted to be conserved in many species, including tobacco, *Populus trichocarpa,* and *Arabidopsis* (Jones-Rhoades and Bartel, 2004). Therefore, miR397 play a greater role in productivity of other crop plants.

Conclusions and Future Prospects

Based on the intensive researches in the past 20 years, rapid and significant progress has been made in uncovering miRNA biogenesis, targets prediction, biological functions, and molecular mechanisms, which greatly advance our understanding about the elaborate and fancy regulatory network generated with long-term plant evolution. In addition, it is a tendency that miRNA can act as a new breeding tool in plant genetic improvement (Zhang, 2015; Zhang and Wang, 2015). As mentioned above, some miRNAs have been proved that possess powerful effect on the regulation of major agronomic characters (Table 1). However, the majority of the miRNA are not well studied, especially some of low-abundance miRNAs, which also exert potent role in plant development as described recently (Wang and Guo, 2015). Additionally, comparing with multifunctional and dominant roles, miRNAs still have many mysterious areas need to be further studied.

In regulatory hierarchy, plant miRNAs prefer to target transcription factors and depend on repressing their transcription factor targets to further regulate the expression of functional genes. However, miRNAs always display various spatio-temporal expression patterns through histochemical and other expression analysis methods. In addition, many miRNAs are rapidly response to different environmental clues.

TABLE 1. miRNA and crop plants agronomic traits

miRNA	Plant species	Functions	Reference
miR156	Cotton	Fiber elongation	(Liu et al., 2014b)
	Rice	Panicle branches, grain yield	(Jiao et al., 2010; Miura et al., 2010)
	Maize	Leaf initiation, floral architecture, tiller	(Chuck et al., 2007a)
	Tomato	Stem pith, fruit size, shorter plastochron, later flowering	(Zhang et al., 2011)
miR172	Rice	Developmental stage, floral organs, fertility and seed weight	(Zhu et al., 2009)
	Maize	Sex determination, meristem cell fate	(Chuck et al., 2007b)
miR828 and miR858	Cotton	Fiber development	(Guan et al., 2014a)
mir397	Rice	Grain yield, panicle branches	(Zhang et al., 2013)

Thus, how the transcript of specific miRNAs be regulated? In addition to that, miR172 can be transcriptionally activated by miR156 target *SPL9*, its expression level also significantly altered in miR172 itself target mutant plants and overexpressing plants. Thus, miRNAs may form a complicated regulatory loop to tightly control miRNA expression despite it still unclear.

In terms of molecular size, miRNAs are the ideal signal molecule for long-distance signaling transduction. Photosynthetic carbon resource and mineral nutrients, which are assimilated in shoot and root, respectively, are two indispensable parts for plant growth and development. In Pi-deficiency growth condition, plant exhibits many growth impairment, such as shortened smaller shoot size, primary, and lateral roots (Devaiah et al., 2007). The communication between shoot and root is essential not only to the plant Pi starvation acclimation but also to keep plant development in a coordinated way (Lin et al., 2008; Liu et al., 2010). Sugars and miR399 have been characterized as two crucial long-distance signal molecules for systemic signaling transduction under Pi-deficient conditions (Liu et al., 2005, 2010; Karthikeyan et al., 2007; Hammond and White, 2008; Lin et al., 2008; Pant et al., 2008). Consistent with this, many small interfering RNAs also usually act as mobile molecules to mediate gene silencing (Dunoyer et al., 2010), and miR394 has been identified as mobile signal molecule to maintain stem cell competence in SAM region (Baumann, 2013; Knauer et al., 2013). In addition, some evidences show that miR172 seems to be implicated as long-distance signals to affect potato tuberization (Martin et al., 2009). Thus, further uncovering the mobile role of miRNAs may help us better understand the interesting regulatory network.

As the sessile nature, plants need to suffer different kinds of biotic and abiotic stresses, such as pathogens infection, drought, heat, cold, and mineral nutrients starvation. However, the plants always need to coordinate the balance between plant development and stresses activation because of the limitation of resources available (Yang et al., 2012a; Fan et al., 2014; Li et al., 2014a). Previous researches demonstrate that transcription factors, depending on the multifunctional transcriptional reprogramming character, play crucial role in the trade-off between development and stresses responses (Pajerowska-Mukhtar et al., 2012; Fan et al., 2014; Li et al., 2014a). Interestingly, just like some transcription factors, some miRNAs appear to implicate in multiple regulations of biological processes, although underlying mechanism still needs to be illuminated. For example, the main floral regulator miR156 and its SPL targets are proved to involve in heat stress memory, salinity, and drought tolerance (Cui et al., 2014; Stief et al., 2014). In addition, recent study show that miR156-*SPL* pathway is able to change the number of lateral root, one of the key organ governing water and nutrients uptake (Yu et al., 2015). Hence, whether miRNAs can function as node molecules, how to converge multiple biological processes for optimal development and thriving are still mysterious for us.

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