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The Regulatory Role of Small RNAs in Plant Development and Defence Mechanism

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Abstract

Small RNAs (sRNAs) are 20 to 40 nucleotides in length and plants use these regulatory RNAs to direct gene expression. In eukaryotes, they act as a sequence-specific guide in several processes like assembly of heterochromatin, DNA elimination, mRNA cleavage and translational repression. Classes of sRNAs are categorized based on their origin and biogenesis. Out of all these, miRNAs and ta-siRNAs, constitute two important classes of endogenous small RNAs, are the ones that mainly inhibit gene expression at post transcriptional levels and have developmental roles in plant which includes growth and development of roots, shoots, leaves, flowers and seeds. They both also have involvement in plant stress response which can be both biotic and abiotic. This review explores the regulatory roles of small RNAs in plant development and defence mechanisms.

Keywords: Small RNAs, defence mechanism, role of miRNA, role of sRNA, plant development, plant immunity, plant stress response, ta-siRNA

INTRODUCTION

Small RNAs (sRNA) are non-coding RNAs. They are 20–40 nucleotide (nt)-long RNA molecules. They are found in a wide range of eukaryotic organisms and play a role in regulating gene expression through sequence-specific mechanisms, operating at both transcriptional and post-transcriptional levels [1–4]. The main work of these sRNA is to regulate post transcription of the target gene and this is accomplished by two processes either by transcript cleavage or translational inhibition. Thus, they help majorly in plant development and in protecting plants from any stress condition or pathogen [5].

Small RNAs are bound by a protein known as argonaute protein. Belonging to an evolutionarily conserved family of proteins, it is identified in bacteria, fungi, plants, and animals. This protein forms an RNA-protein complex with sRNA known as RISC (RNA induced silencing complex), that helps in silencing function. Argonaute proteins are of two types: one subfamily is associated with miRNA and siRNA and the other one is associated with piRNA (Piwi-interacting RNA). The latter is not found in plants, both RNA and protein (piwi subfamily) [6].

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sRNAs are majorly classified as miRNAs (microRNAs) and siRNA (small interfering RNA). siRNAs again are then classified into four types: natural antisense transcripts (NATs)-derived siRNAs known as nat-siRNAs, lsiRNA (long siRNAs), ra-siRNA (repeat-associated si-RNAs) or hc-siRNAs (heterochromatic siRNAs) and ta-siRNAs (trans-acting si-RNAs). nat-siRNAs and miRNAs contribute to plant antibacterial immunity [7, 8]. hc-siRNA has a role in epigenetic modification of chromatin in the target locus, thus helping in silencing of genes via transcription [5]. ta-siRNAs are 21 nucleotide sRNA, that cleaves non identical targets and thus the name [9].

miRNAs are the subsets of shRNA (hairpin RNAs) which are the artificial RNAs that silence gene by RNAi. They were discovered in non-parasitic nematodes. *Caenorhabditis elegans* have highly precise excision of functional products. They are conserved over long evolutionary sequences. When compared to siRNA, miRNAs are present in a very small amount [10, 11]. siRNAs are the majority of the small RNA that are present in the biological world and the difference between miRNA and siRNA is in its biogenesis.

miRNAs are produced from RNA polymerase II-derived transcripts of miRNA genes. The first structure that forms is the primary miRNA, which is further processed into forming precursor miRNA. DDL protein recruits DCL1(DICER like protein 1) which acts on primary miRNA for the formation of precursor miRNA. Then DCL1 along with HYL1 (HYPONASTIC LEAVES 1) and SE (SERRATE) help to form small RNA duplexes and further process pre-miRNA to finally form miRNA duplex [12–14]. This duplex is then methylated at its 3' ends by HEN1 (HUA ENHANCER 1) and is exported later to cytoplasm by HST (HASTY), an exported homolog [15].

siRNA are derivatives of perfectly base-paired hairpin loop structures unlike miRNA. They originate from either antisense transcription or through the activity of cellular RNA-dependent RNA polymerase (RDR). TAS genes are transcribed by RNA polymerase II to produce long non-coding transcripts which are cleaved by miRNAs loaded with RISC thereby resulting in 5' and 3' fragments.

In the field of plant biology, there has been a substantial increase in scientific research in recent years, focusing on the pivotal role of sRNAs in both plant development and defence mechanisms. Within this context, numerous researchers have made valuable contributions by presenting excellent studies on the involvement of sRNAs in the development of various plant components and in plant defence mechanisms [16, 17]. Hence, this review will encompass an in-depth exploration of present insights and recent advancements pertaining to the function of sRNAs and their engagement in both plant defence mechanisms and developmental processes.

ROOT DEVELOPMENT

The root system in plants originates from RAM, whose meristematic cells go into cell division and differentiation [18]. Root development mediated by si-RNA in plants happens by different RNAs targeting transcription factors or genes that are involved in development of different kinds of roots. Majority of these studies have happened in angiosperms particularly in *Arabidopsis.* In a fully developed root system in dicots, the observed roots are adventitious roots, lateral roots and primary roots; whereas in monocots, roots observed are crowned roots, seminal roots, primary roots and lateral roots. PR and SR are embryonic roots whereas the rest others are post embryonic [18].

miR160 is required for root growth and its branching [19]. It essentially inhibits the elongation of root and the development of root cap [20]. This happens by targeting and repressing ARF10, ARF16 and ARF 17; this inhibits LR development as the AIR3 gene is not promoted [20]. miR160 also helps in development of adventitious roots and here it targets only ARF17 and represses it, whose expression and accumulation causes negative regulation of adventitious roots [21, 22].

miR164 regulated the emergence of LR and its branching by regulation of certain transcription factors which are NAM/ATAF/CUC1(NAC1) [23]. miR164 accumulation happens at the later stage of auxin treatment in *Arabidopsis* [23]. miR167 contributes to the positive regulation of certain ARFs that are responsible for the positive regulation of adventitious roots; ARF6 and ARF8 (4). This miR167 works alongside miR160 in a loop to ensure a balance in the number of adventitious roots [21, 22].

miR165/166 helps in vascular tissue development and root growth [24]. This starts by SHORT-ROOT (SHR) transcription factor production in the stele region of root. SHR then moves to the outward endodermis where it activates the expression of another transcription factor SCARECROW (SCR). In

endodermis, SCR and SHR both promote the expression of miR165/166. This sRNA moves radially to both inwards stelar region and outwards and degrades Class III (HD-ZIP) HOMEODOMAIN-LEUCINE ZIPPER transcripts [24]. miR165/166 regulates the root growth by phytohormonal crosstalk [25].

miR396 studied in *Arabidopsis* regulates the stem cell niche (SCN) [26, 27]. SCN contains infrequently dividing cells i.e., the quiescent centre surrounded by mitotic initials, thus the root tip [28]. It targets GROWTH RESPONSE FACTORS (GRFs) and regulates cell division [26, 27]. This RNA regulates the switch that controls transition from stem cells to transit-amplifying cells (TACs) [27]. miR 396 is expressed in only stem cells and not in TACs. This allows accumulation of GRFs in the TACs and GRFs repress the expression of PLETHORA (PLT) in the TACs, thereby repression of miR396 [27]. On the other hand, in Stem cells, there is a lack of GRFs which causes expression of PLT and thereby activating miR396 expression [27]. Thus, this way a regulatory circuit is established.

miR171 also plays a role in the maintenance of stem cells. It has been observed in *Arabidopsis* and *Medicago,* that repression of LOMs/HAIRY MERISTEM (HAM) which is miR171 mediated impairs the growth of primary root and stem cell maintenance [29–31]. miR847 controls the number of LR by controlling the expression of IAA28 (INDOLE ACETIC ACID 28), studied in *Arabidopsis.* IAA28 is a repressor of auxin inducible gene. Reduced expression of IAA28 results in an elevated number of lateral roots (LRs) [32].

miR393 also controls LR development by modulating auxin-signalling pathway. This phenomenon has been investigated in both *Arabidopsis* and rice. In these cases, the sRNA targets TRANSPORT INHIBITOR RESPONSE PROTEIN 1 (TIR1) as well as AUXIN SIGNALLING F-BOX PROTEIN 1 (AFB1), AFB2, and AFB3. Any disruption in this pathway leads to defects in LR development [33–35]. Both miR408 and miR528 regulate the formation of root cap, root elongation and LR development by targeting CUPREDOXIN [36].

Ta-siRNA also plays an importance in root development. It works alongside miR390. Here, auxins and ARFs induce miR390 expression which leads to production of TAS3 ta-siRNAs that restrict the expression of ARF2, ARF3 and ARF4. This loop helps to maintain concentration of ARFs to specify timing for LR growth [37, 38]. TAS3a overexpression increases LR length and mutation decreases it [37]. The auxin maxima is sensed by miR390 and ARF4 expression is inhibited by TAS3a derived ta-siRNA [37, 38].

SHOOT AND LEAF DEVELOPMENT

The shoot apical meristem (SAM) comprises a cluster of meristematic cells that serve as the origin for all aerial organs in plants. It is specified early in embryonic development. Several miRNAs contribute to SAM development, organisation and maintenance which can be achieved by regulation of many targets [39].

The initial indication of the significance of sRNAs in plant development arose from the discovery of a dominant allele of the *Arabidopsis* class III HOMEODOMAIN LEUCINE ZIPPER (HD-ZIP III) transcription factor, PHABULOSA (PHB). This allele disrupted leaf polarity and led to abnormal meristem formation on leaves [40]. Elevated activity of miRNA165/miR166, coupled with a concomitant decrease in HD-ZIP III expression, results in the loss-of-function mutations within the AGO family member, PINHEAD/ZWILLE/AGO10, leading to an aborted embryonic shoot apical meristem (SAM) phenotype [41–43]. AGO10 functions by sequestering members of the miRNA165/166 family, thereby preventing their interaction with AGO1, the principal mediator of miRNA-induced gene repression in Arabidopsis [44, 45].

The shoot apical meristem (SAM) is compartmentalized into three distinct layers (L1, L2, L3). Within the innermost layer (L3), a specific cluster of cells expresses the transcription factor WUSCHEL (WUS). In this location, WUSCHEL (WUS) fosters the proliferation of these cells [46]. miR394 is

initially expressed in the outermost protoderm (L1) layer, and from there, it diffuses to establish an expression gradient that coincides with the expression domain of its target, the F-Box protein LEAF CURLING RESPONSIVENESS (LCR) [47]. Plants lacking miR394 and plants expressing LCR alleles resistant to miR394 illustrate that the suppression of LCR by miR394 is crucial for stem cell proliferation. Additionally, it plays a vital role in sustaining the embryonic shoot apical meristem (SAM), a process dependent on the coordinated intercellular movement of both WUS and miR394 [47].

miR396 curtails cell proliferation by suppressing the GROWTH REGULATING FACTOR (GRF) family of transcription factors. Enhanced expression of miR847, which targets IAA28, leads to prolonged cell proliferation [44]. Moreover, perturbed function of the auxin-receptor regulator miR393 has an impact on leaf morphology in both *Arabidopsis* and rice [48, 49]. As leaves mature, the expression of miR396 rises, and the equilibrium between miR396 and GRFs determines whether cells undergo mitosis or remain in interphase [50–52]. The escalation in miR396 expression during leaf aging not only functions as a signal to halt cell proliferation but also contributes to the induction of leaf senescence [53].

In addition to these genes, the NO APICAL MERISTEM/CUP SHAPED COTYLEDON (NAC) genes play a role in defining the demarcation between the meristem and the adjacent cotyledons [54]. Plants with dual mutations in the genes cuc1 and cuc2 exhibit fused cotyledons and a complete absence of a shoot apical meristem (SAM) [55]. CUC1 and CUC2 are primarily targeted by miRNA164 in various plants such as *Arabidopsis, Solanum,* and *Oryza* [56]. Expression of this gene results in a shoot meristemless phenotype when considering the CUC1 and CUC2 double mutants [56]. Plants expressing a miR164-resistant form of either CUC1 [57] or CUC2 [56], along with plants with significantly reduced miR164 activity [58], display anomalies in leaf serration but otherwise exhibit a relatively normal appearance during the vegetative stage of shoot development. Moreover, miR156 focuses on various members belonging to the group of transcription factors known as SQUAMOSA PROMOTER BINDING PROTEIN (SBP/SPL). These transcription factors play a pivotal role in facilitating the development of mature characteristics [59–64], and they also contribute to translating the influences of environmental pressures into developmental changes in shoots [65–68]. Elevated miR156 concentrations suppress the expression of SPL during initial development. As miR156 levels diminish throughout shoot maturation, the expression of SPL genes escalates, consequently leading to the transition of the vegetative phase. In the case of *Arabidopsis*, miR156 takes a direct aim at 11 SPL genes, with evidence from loss-of-function mutations in SPL9 and SPL15 indicating their significant involvement in the process of vegetative phase change [69, 70]. Furthermore, miR172 directs its attention towards AP2 and forms a connection close to the transcriptional start points of both AGL15 and MIR156E. This observation proposes that genes positioned downstream of miR156 might potentially influence its expression through a feedback mechanism [70, 71].

miR319 is focused on genes associated with TEOSINTE BRANCHED1/CYCLOIDEA/PCF (TCP) transcription factors, which play a role in encouraging cellular differentiation and inducing mitotic arrest. Additionally, miR319 governs the process of leaf senescence in angiosperms [72–74]. When miR319 is overexpressed, it triggers the enlargement of the leaf blade and intensifies the curvature of the leaf [75, 76]. Conversely, the disruption of miR319 regulation, coupled with the resulting rise in CIN-TCP expression, precipitates early differentiation, diminished cell proliferation, and a simplification of leaf structure [77–79]. In *Arabidopsis*, it diminishes the responsiveness to cytokinin [80] and encourages the efficacy of gibberellin [81]. CIN-TCPs additionally stimulate the upregulation of miR396 [79] and miR164 [78, 82], along with elements of the ta-siRNA pathway. Moreover, they play a role in triggering senescence through the jasmonic acid pathway.

In double mutants of miR159a/b, MYB33 and MYB65 exhibit decreased cell proliferation in leaves due to their function [83]. Moreover, due to their impaired pollen production, MYB33 and MYB65 double mutants do not display any noticeable vegetative phenotype. Consequently, translational reporters of MYB33 and MYB65 exhibit no expression in leaves, indicating their detrimental impact

on vegetative development. This implies that the role of miR159 is to suppress their expression during this developmental stage. In the majority of plant species, it has been demonstrated that loss-of-function mutants of ta-siARF targeting ARF2 result in a postponement of senescence [84, 85]. Further, it also limits abaxial leaf development, and represses the adult leaf traits.

SEED DEVELOPMENT AND GERMINATION

The ovules in the plant turn into seeds which is an evolutionary adaptation for germination when the favourable conditions appear and dispersal [86, 87]. This stands as a pivotal characteristic in agriculture. Certain genes are present in the sRNA pathway which may go under mutation and cause severe defects in the embryogenesis and seed development, like DCL1(1). Different miRNAs have different stages where they regulate embryonic development from pre-globular to mature embryonic stages.

miR160 targets ARF10/16/17 (Auxin Response Factor). It is a common miRNA in both germination and seed development. This small RNA when goes into an overexpression causes ABA (Abscisic acid) hyposensitivity. Mutation in ARF10 causes seed developmental defects [88]. On the other hand, studied in *Arabidopsis*, miR402 overexpression under certain stress conditions, like cold, salt and osmotic, leads to enhancement in seed germination [89]. miR417 is a negative regulator for seed germination in *Arabidopsis* [90, 91].

In rice, it has been studied that miR156 and miR396 are regulators of grain size since these RNAs target genes SPL6 and GRF4 respectively [92, 93]. Genetic mutations in these genes lead to amplified grain size and enhanced yield [92–94]. miR397 is also a positive regulator for rice fields.

An intensified response to ABA is observed in seed germination and initial seedling growth when short tandem target mimicry of miR165/166 (STTM 165/166) is in effect [95]. miR395 is both a positive and negative regulator of germination. miR156 and miR172 are master regulators in seed germination and phase transition [96]. miR158, miR160, miR164, miR165/166 and miR167 help in maintaining an auxin homeostasis which is crucial for seed development [97]. Table 1 lists the major targets and functions of small RNAs involved in regulation of plant development and defence mechanisms.

FLOWER DEVELOPMENT PATTERN AND PHASE TRANSITION

Flowers contain the reproductive organs of the plant and their development. During the floral development, a gradient between two miRNAs is maintained, these are miR156 and miR172. During the juvenile stage of the plant, the former RNA's concentration is high which decreases as the flower becomes adult and later reaches reproductive maturity whereas the latter RNA's concentration increases. Ectopic miR156 expression will cause delayed flowering [98, 99]. Both miR156 and miR157 regulate floral timing negatively by targeting SQUAMOSA-PROMOTER BINDING PROTEIN LIKE (SPLS) [98, 100]. There are 17 SPLs encoded in *Arabidopsis* which are targeted by miR156 [99, 101].

In studies, maize and *Arabidopsis*, miR172 targets the AP2 transcription factor family, and a small group of AP2-like genes {TARGET OF EAT1 (TOE1), TOE2, TOE3, SMZ (SCHLAFMÜTZE), and SNZ (SCHNARCHZAPFEN)} downregulate it, thereby accelerating floral transition. Developmentally, it specifies the identities of different floral parts like perianth, sepals, and petals [102, 103].

LEAFY gene when targeted by miR159 controls floral timing by floral meristem regulation. This is achieved by negative regulation of MYB transcription factor families (MYB33, MYB65 and MYB101) which mediate Gibberellic acid induced regulation of LFY [104, 102]. Overexpression causes delayed flowering. It is also responsible for male sterility. miR171, studied in *Arabidopsis*, regulates SCARECROW LIKE (SCL) SCL6-III and SCL6-IV [104, 103].

Table 1. Targets and functions of small RNAs involved in regulation of plant development and plant defence mechanisms.

Development	siRNAs/miRNAs	Species	Targets	Functions
Seed development and germination	miRNA160	*Arabidopsis*	ARF10,16,17	Overexpression causes ABA hyposensitivity
	miRNA156 and 172			Master regulator of phase transition and seed germination in plants
	miR402	*Arabidopsis*		Enhance seed germination under salt, osmotic and cold stress
	miR395			Both positive and negative regulator of seed germination
	miR417	*Arabidopsis*		Negatively regulate seed germination during salt stress
	miR165/166 (STTM 165/166)			ABA hypersensitivity during seed germination, Auxin homeostasis
	miR167, miR164, miR158			Auxin homeostasis
	miR164		CUC1, CUC2	Embryonic and floral organ fusion
Root development	miR160	*Arabidopsis*	ARF10,16,17	Growth, branching regulation by negative regulation of target genes, increased lateral roots
	miR164	*Arabidopsis*	NAM/ATAF/CUC1 (NAC1	Lateral root (LR) emergence and branching
	miR167		ARF6 and ARF8	Positive regulation of adventitious roots
	miR393		TIR1 and AFB2	LR growth
	miR165/166	*Arabidopsis*, Maize	HD-ZIP III	Vascular differentiation and root growth
	miR396		GRFs (Growth response factors)	Cell division
	miR171		hairy meristem (HAM)	Ectopic expression affect primary root (PR) length, HAM mutation causes defective quiescent centre and shunted root growth
	miR847		IAA28	LR development and number
	miR408		CUPREDOXIN	Root cap formation, LR development and root elongation
	miR528		CUPREDOXIN	Root cap formation, LR development and root elongation
	tasi-ARF	*Arabidopsis*	ARF3, ARF4, miR390	LR growth
	tasi3a	*Arabidopsis*		Overexpression increases LR length and mutation reduces LR length
Flower development	miR156/157	*Arabidopsis*, Maize	SPLs	Regulate floral timing, Vegetative growth change and floral transition, prolong vegetation if overproduction
	miR159		LFY (LEAFY gene), SPL, MYB	Control floral timing by regulating floral meristem by negative regulation of GA, Male sterility, late flowering
	miR171	*Arabidopsis*	inflorescence	Regulate SCL6-III and SCL6-IV
	miR172	Maize	AP2-like gene GLOSSY15(GL15), TOE1	Juvenile to adult shoot transition, Stimulates flowering, late flowering
	miR172b		TOE1	Early flowering
	miR396			Regulate floral identity and timing

	miR167	*Arabidopsis*	ARF6, ARF8	Causes sterility if the targets are resistant, male organ development
	miR169	*Antirrhinum majus*	CBF	Enhancer of C homeotic gene transcription
	miR390	*Arabidopsis*	TAS3	tasi RNA biogenesis for ARF repression and indirect miR165/166 regulation
	miR160			Pollen development
	miR173			Pollen development
	miR319	*Arabidopsis*		Modest delay in flowering time
Trichome development	miR156		SPLs	Overexpression causes ectopic trichome development
	miR171		LOMs (Lost Meristems)	Results in fewer trichomes than miR156
Hormones	miR159		MYB33, MYB65, and MYB101	Activate GA response gene, overproduction delayed flowering and male sterility, mutation causes ABA hyposensitivity
	miR160		ARF 10, 16, 17	Resistance causes pleiotropic developmental defects in aerial organs
	miR167		ARF 6 and 8	Regulate ovule and anther development
	miR319		ARF 3 and 4	Promote abaxial identity of lateral organs as well as the expression of adult vegetative traits in leaves
Shoot and Leaf development	miR156	*Arabidopsis*, *Zea mays*	SPL family	Repress vegetative phase change, Plastochron regulation.
	miR172	*Arabidopsis*, *Zea mays*, *H. vulgare*, and *S. tuberosum*	AP2 family	Promote adult leaf morphology.
	miR165/166	*Arabidopsis*	HD-ZIP III	Limit adaxial leaf development, Restrict meristematic growth.
	miR164	*Arabidopsis*, *Solanum* and *Oryza*	NAC family, CUC1 and CUC2	Regulate leaf serration/complexity, Delay senescence.
	miR394	*Arabidopsis*	LCR,	Embryonic SAM maintenance.
	miR396	*Arabidopsis*, *Medicago*, and *Oryza*	GRF family	Limit cell proliferation, Promote senescence.
	miR319	Tomato, *Arabidopsis*	TCP family	Promote cell proliferation, Delay senescence.
	miR159	*Arabidopsis*	MYB Family	Limit cell proliferation.
	miR393	*Arabidopsis*	TIR1 and AFB	Auxin homeostasis.
	miR857	*Arabidopsis and Citrus sinensis*	LACCASE7	Secondary growth.
	ta-siARF	*Arabidopsis*, All land plants	ARF2/3/4	Limit abaxial leaf development, Delay senescence, Repress adult leaf traits.
Innate Immunity/Stress Response	miR393	*Arabidopsis*, (infection by *Pseudomonas syringae*)	Auxin signalling receptors such as AFB genes traits.	Pathogen-triggered immunity (PTI) confers resistance against the bacterial pathogen *Pseudomonas syringae* pv. tomato (Pto) DC3000.
	miR159	*Arabidopsis*	Target MYB101 and MYB33 transcripts	Regulating the JA biosynthesis pathway.

	miR393	Rice (*Oryza sativa*)	Regulates the expression of auxin receptor gene homologs (OsTIR1 and OsAFB2)	Early flowering, hyposensitivity to auxin, and reduced tolerance toward drought and salt stress.
	miR160a	Rice	Higher accumulation of H_2O_2 at the infection site and an induction of defence gene expression against blast fungus disease	Accumulation of callose.
	miR167	*Oryza* (infection by *Agrobacterium tumefaciens)*	expression at the infiltration regions	Plant defence
	miR398	*Arabidopsis* (infection by *Pseudomonas syringae*)	Targets and regulates the expression of two of three Cu/Zn Superoxide dismutase (SOD) transcripts (CSD1 and CSD2).	Protect cells from the oxidative stress associated with pathogen infection
	miR390	*Arabidopsis*	TAS3, ARF3 and ARF4	Auxin signalling
	miR398 and miR773 a	*Arabidopsis* (infection by *Pseudomonas syringae*)	Negative regulators of PAMP	Negative regulators of PAMP-induced callose deposition, and by modulating the deposition of callose, disease resistance
	miR167, miR171, miR408, miR444, and miR1138	Wheat (*T. aestivum*) (by *Blumeria graminis,*)	Not given	Triggers the production of many miRNAs in wheat (*T. aestivum*) and, among these, miR167, miR171, miR408, miR444, and miR1138 are involved in PTI
	R proteins	*Solanum Lycopersicum (*infection of *Cladosporium fulvum*)	cf family	R gene-mediated defence mechanism, also referred to as ETI, resistance to the fungus *Cladosporium fulvum*
	miR6022	Potato	LRR-RLKs	Downregulation of GA signalling
	miR482 and miR2118	Tomato	R genes	Regulate R genes of the NBS-LRR type
	miR482 and miR5300	Tomato (infection by *Fusarium oxysporum)*	NB domain genes and tm-2	Defence (resistance)
	miR472	*Arabidopsis*	NBS-LRR (CC-NBS-LRR) genes	Regulating the PTI and ETI responses
	miR9863	Barley	Mla alleles, which encode CC-NBS-LRR receptors	Resistance against powdery mildew fungus
	miR863-3p	*Arabidopsis*	ARLPK1 and ARLPK2	Forming a negative feedback loop to attenuate plant immunity, Improve the defence responses
Environmental stress responses	miR395	*Arabidopsis*	ATP sulfurylase APS4 enzyme	Assimilation of inorganic sulphates and accumulates in low-sulphur conditions

	miR393 and miR319c		Environmental Stress (increased expression levels during exposure to different stress factors)	Protection system of plants for structural and mechanical fitness
	miR389a, miR397b, and miR402		Environmental stress (declined under stress treatments including cold, dehydration, salinity, and ABA)	Protection system of plants for structural and mechanical fitness
	miRl59		GA and ABA expression	Development of Flower
	miRNA159	Tomato	Downregulated under cold, ABA, and NaCl treatments	Impact stress tolerance
	miRNA166	Tomato		Altered expression pattern in root and hypocotyl tissues
	miR159, miR472, and miR482	Tomato		Inversely expressed in the hypocotyl compared with roots
	miR444	Rice	Transcripts encoding MIKC-type MADS box proteins, MADS23, MADS27, and MADS5, which are transcriptional repressors of the RDR1 gene	Boost RNA-silencing against the virus.
	miR528	Monocots	SPL9	Tolerant interaction of rice to RSV, Negative regulator
	miR156	*Nicotiana and Arabidopsis*	SPL9	Negative effector of immunity, regulating ROS accumulation and activating the salicylic acid (SA) Signalling pathway
	miR319	Monocots		Negatively regulates tolerance responses of rice to rice ragged stunt virus and of wheat to RBSDV, overexpression facilitates infection and symptom development, whereas blocking its activity results in milder symptoms and lower virus levels
	miR156 and miR319, miR166	Dicots and Monocots		Regulatory role in antiviral responses
	miR166	Dicots		Attenuates symptom development.
Symbiosis	miR5213, miR5281	AM symbiosis in *Medicago truncatula*	R genes (NBS-LRRs)	Immune responses to tolerate invasion and proliferation of beneficial microorganisms
	miR482,	Soyabean	NBS-LRR transcripts	Establishment of symbiosis between soybean and *Bradyrhizobium japonicum*
	miR160, miR164, miR167, miR390, and miR393, miR169, miR171 and miR319,	Potato		Regulated during tolerance response of potato to PVY, regulate nodulation and AM symbiosis in different legume species, MiR171 was linked to tolerance in several viral pathosystems

	miR171	Rice	RSV	Overexpression: shows attenuated disease symptoms, reduction: accumulation leads to development of disease symptom
Synthesis of secondary metabolites for plant defence	miR-156a, miR-166a, miR-168, and miR-11320	*Arabidopsis*	Target metabolic enzymes, such as acetyl-CoA acetyltransferase, aspartate aminotransferase, premnaspirodiene oxygenase, and phosphoglycerate mutase	Synthesis of Secondary metabolites
	Light-stimulated miRNAs	Tomato		Regulators of lipid biosynthesis, alkaloid metabolism, and cellulose catabolism
	miRnas	*Brassica napus*	Stress with cadmium	Regulation of the biotic stress response, transcription factors and secondary metabolite synthesis
	miR858a	*Arabidopsis*	MYB transcription factors	Flavonoid biosynthesis pathway.
	miR477 and miR530 in leaf and miR159 and miR5140 in root	*Withania somnifera*		Regulating the synthesis of secondary metabolites.
	miR8154 and miR5298b	*Withania somnifera*		Synthesis of flavonoids and phenylpropanoids in subcultured Taxus cells.
Reproduction	heterochromatic siRNAs	*Arabidopsis*,	AGO9	Loss of function of AGO9, which encodes a member of the AGO4-clade that associates with heterochromatic siRNAs, results in ovules with multiple MMCs.
	heterochromatic siRNAs	Maize	AGO4-clade member ago104	Loss of function causes defects in chromosome condensation and chromosome segregation during meiosis of the MMC
	ta-siRNAs.	*Arabidopsis*	rdr6 and sgs3	Exhibit partially penetrant female germ line defects similar to ago9 mutants
	phasiRNAs	Rice and Maize	MEL1	Promote germline specification or meiosis, exhibit meiosis defects

miR167 regulates floral development by targeting ARF6 and ARF8 [105, 106]. A resistant plant to the function of this RNA will deal with sterility as mutation of ARF6 and 8 causes defective stamen filament and pollen. It was phenocopied by miR167 overexpression [105, 106].

miR169 studied well in *Antirrhinum* and *Petunia* controls AG homologous expression. Its target is the CCAAT box binding factor (CBF) family that is required for transcription of C gene whose expression is done by entire flower primordium. Thereby it controls the ABC genes expression during flower organ identity specification [107].

TRICHOME DEVELOPMENT

Trichomes are certain protuberances on the epidermis of the aerial part of plants. They generally have protective functions in plants like transpiration, radiation or certain herbivore attack [108]. Its development in plants is regulated by the interplay of two miRNAs: miR156 and miR171. They target SPL and LOMs, which cause an increase and decrease in the number of trichomes, respectively [109, 110]. These trichomes develop on the stem and floral organs of the plant.

INNATE IMMUNITY/STRESS RESPONSES

Pathogen-triggered Immunity

In *Arabidopsis*, it has been established that miRNAs play a role in the response to PTI. When subjected to flagellin22 treatment, there is a notable rise in the levels of miR393. This miRNA, in turn, suppresses the expression of genes responsible for coding auxin signalling receptors, specifically the AFB genes. Overexpressing miR393 in plants leads to the inhibition of auxin signalling and confers resistance against the bacterial pathogen *Pseudomonas syringae* pv. tomato (Pto) DC3000. Conversely, plants with a constant expression of AFB1 exhibit accelerated growth of Pto DC3000 bacteria [111]. These findings offer substantial evidence of a well-defined molecular link between miR393 and auxin signalling within PTI responses. They highlight how both direct and indirect hormonal regulations of miRNAs can intricately modulate plant defence mechanisms in response to pathogen infections.

The influence of miR393 on auxin signalling is likewise evident in *Oryza sativa*. This is apparent through the regulation of auxin receptor gene counterparts (OsTIR1 and OsAFB2) by miR393. Overexpressing miR393 leads to outcomes such as early flowering, reduced responsiveness to auxin, and heightened vulnerability to drought and salt stress. Moreover, several other bacterium-regulated miRNAs, including miR160 and miR167, assume significant functions in plant defence mechanisms [112, 113]. In *Oryza sativa*, elevating the levels of miR160a leads to increased accumulation of H_2O_2 at the site of infection, along with the activation of defence gene expression against blast fungus disease [114]. The expression of miR167 undergoes regulation upon *Agrobacterium tumefaciens* infection. Specifically, an oncogenic strain of *Agrobacterium tumefaciens* triggers the upregulation of miR167 expression at the infiltration sites. Conversely, a strain lacking tumorigenic characteristics fails to induce the expression of miR167 [115]. Furthermore, miR160a functions as a positive regulator, while miR398 and miR773 operate as negative regulators of PTI. They collectively influence the deposition of callose, contributing to resistance against *P. syringae*. These miRNAs collectively confer disease resistance against *P. syringae* in *Arabidopsis* [114]. The ABA signalling pathway experiences regulation by miR159 via its targeted transcripts, MYB101 and MYB33. Conversely, miR319 targets the TCP transcription factor which is engaged in the regulation of the JA biosynthesis pathway [116].

miR398 exhibits changes in its expression pattern during bacterial infection. It functions by targeting and controlling the expression of two out of three Cu/Zn Superoxide dismutase (SOD) transcripts, specifically CSD1 and CSD2 [117]. Upon infection by avirulent strains of Pst DC3000 (avrRpm1 or avrRpt2) in *Arabidopsis*, a reduction in the abundance of miR398 is observed. Simultaneously, there is an elevation in the transcript levels of CSD1 and CSD2, along with a mitigation of oxidative stress levels. In *Oryza sativa*, overexpressing miR398b leads to an increased accumulation of H_2O_2 at the site of infection. This, in turn, triggers the induction of defence gene expression, including the activation of PR1 and PR10 genes.

Upon infection by *P. syringae* in *Arabidopsis*, there is a decline in miR390 expression. This decrease is followed by an elevation in the expression levels of TAS3, which in turn triggers the generation of ta-siRNAs. These ta-siRNAs play a role in directing the regulation of ARF3 and ARF4 genes, which are essential components of auxin signalling [118]. Overexpressing miR400 or miR844 in *Arabidopsis* results in heightened susceptibility to *Pseudomonas syringae* pv. tomato DC3000 and the fungus *Botrytis cinerea* [119]. The powdery mildew fungus *Blumeria graminis* prompts the generation of numerous miRNAs in wheat (*Triticum aestivum*). Notably, miR167, miR171, miR408, miR444, and miR1138 play roles in plant immune responses, specifically in Pattern-Triggered Immunity (PTI) [120].

Effector-triggered Immunity

R proteins possess solely an extracellular leucine-rich repeat (LRR) domain. This is exemplified by the proteins of the Cf family found in *Solanum lycopersicum*, which grant resistance against the fungus *Cladosporium fulvum* [121]. Under normal circumstances, R-protein activity and abundance are deliberately kept at a lower level to conserve resources for plant growth and development. In

Arabidopsis, a case in point is the downregulation of R genes within the *Peronospora parasitica* 5 (RPP5) locus, which is triggered by the overexpression of SUPPRESSOR OF NPR1-1, CONSTITUTIVE 1 (SNC1). For instance, mutants that lack functional small RNA (sRNA) biogenesis machinery, like dcl4-1 and ago1-36, exhibit elevated levels of SNC1 transcripts. This suggests that during pathogen infection, the expression of SNC1 is held in check through an sRNA pathway, likely facilitating the expression of R genes [122].

Within *Nicotiana benthamiana*, miR6019 and miR6020 play a regulatory role in TIR NBS-LRR (TNL)-type receptor genes. Cleavage resulting from these interactions leads to the generation of 21-nt phasiRNAs. These phasiRNAs are instrumental in suppressing R genes, thus contributing to the modulation of immune responses. An excessive abundance of miR6019 and miR6020 leads to the attenuation of TIR-NBS LRR protein N-mediated resistance against tobacco mosaic virus in *Nicotiana benthamiana* [123].

The miRNA superfamilies miR482 and miR2118 are also involved in the regulation of NBS-LRR type R genes in *Solanum lycopersicum* (tomato) [124]. Through bioinformatics-driven analysis, it was inferred that miR482 targets 58 out of the 168 R genes, with a preference for coiled-coil (CC)-NBS-LRR (CNL) mRNA transcripts [124]. miR482 is anticipated to bind within the P-loop region of the transcript, enabling it to regulate a broader set of NBS-LRR genes. This, in turn, prompts the production of phasiRNAs, which culminate in the concurrent suppression of R genes [125]. In *Solanum lycopersicum*, following treatment with the fungal pathogen *Fusarium oxysporum*, the miRNAs miR482 and miR5300 experience induction. These two miRNAs are responsible for targeting the three NB domain genes. The pronounced expression levels of these genes in resistant cultivars, as opposed to susceptible ones, imply that the regulation of NB genes through miR482/miR5300 holds significant importance in imparting fungal resistance in tomatoes [126]. miR472 has been demonstrated to play a role in governing both Pattern-Triggered Immunity (PTI) and Effector-Triggered Immunity (ETI) responses in *Arabidopsis*. It achieves this through post-transcriptional modulation of NBS-LRR (Coiled-Coil Nucleotide-Binding Site Leucine-Rich Repeat) genes [127]. Furthermore, the miR9863 family serves as a catalyst for producing 21-nt long phased small RNAs (phasiRNAs). These phasiRNAs establish a regulatory framework that suppresses the expression of group 1 Mla alleles. These alleles encode Coiled-Coil Nucleotide-Binding Site Leucine-Rich Repeat (CC-NBS-LRR) receptors. This regulatory mechanism also extends to different Mla alleles in barley. Moreover, elevating the expression of miR9863 results in a reduction of MLA1-triggered resistance against the powdery mildew fungus [128].

The expression of miR863-3p significantly increases following Pst (avrRpt2) infection. This microRNA plays a crucial role in downregulating both negative and positive regulators of plant immunity using distinct mechanisms. Initially, miR863-3p targets typical receptor-like pseudokinase 1 (ARLPK1) and ALPK2 by facilitating mRNA degradation. This degradation enhances the plant's defence responses post-infection. Notably, ARLPK1 engages with AKIK1, establishing a negative feedback loop. This loop serves to dampen immune responses once the defence mechanisms have effectively functioned. Subsequently, miR863-3p also diminishes the levels of SERRATE (SE) through translational inhibition. This action serves to weaken defence signals that rely on SE accumulation. As a result, a negative feedback loop is established, contributing to the modulation of plant immunity and its attenuation [129].

In rice, miR444 promotes tolerance to rice stripe virus (RSV) infection. It reduces accumulation of its targets, MADS23, MADS27, and MADS5, which are transcriptional repressors of the RDR1 gene, thus boosting RNA-silencing against the virus. miR444 overexpression results in milder symptoms and reduced accumulation of RSV [130]. Another monocot specific miRNA, miR528, is involved in tolerance of *Oryza* to RSV. miR528 is a negative regulator, cleaving L-ascorbate oxidase (AO) mRNAs, thereby reducing AO-mediated accumulation of reactive oxygen species (ROS). ROS is an important

signalling component in antiviral immunity [131]. miR528 mutant plants displayed milder symptoms and accumulated less virus, whereas miR528 overexpression lines were more susceptible to RSV infection [132]. miR528 was found to be negatively regulated by the ROS, hydrogen peroxide [133], indicating that redox homeostasis is important in promoting tolerance. In diseased maize, miR528 was upregulated after sugarcane mosaic virus infection, while miR444 was downregulated, further supporting their role as positive and negative regulator of antiviral immunity in monocots.

In dicots, miR156 functions as a negative effector of immunity. Increased levels of miR156 were found to correlate with severity of disease symptoms in *Nicotiana benthamiana* in response to potyviruses potato virus Y (PVY) and plum pox virus [134]. Similarly, miR156 levels were increased by tobacco mosaic virus, which causes the symptom severity in *Nicotiana tabacum* [134]. In *Arabidopsis*, miR156 suppression mutants or SPL9 overexpression mutants exhibited increased ROS levels and decreased expression of SA signalling genes [135].

In monocots, by contrast, miR319 negatively regulates tolerance responses of rice to rice ragged stunt virus and of wheat to RBSDV. miR319 overexpression facilitates infection and symptom development, whereas blocking its activity results in milder symptoms and lower virus levels [136]. Similar to miR156 and miR319, miR166 is another conserved miRNA that displays a contrasting regulatory role in antiviral responses in monocot and dicot species. In dicots, suppression of miR166 expression attenuates symptom development [137–139]. On the other hand, decreased miR166 levels were detected in symptomatic virus-infected rice and maize.

miRNAs Producing Secondary Metabolites in the Defence Response

Transcriptome analysis of *Swertia* plants has identified a set of miRNAs linked to the regulation of secondary metabolite synthesis. Notable among these are miR-156a, miR-166a, miR-168, and miR-11320, which have been found to target key metabolic enzymes. These enzymes include acetyl-CoA acetyltransferase, aspartate aminotransferase, premnaspirodiene oxygenase, and phosphoglycerate mutase. Additionally, miR393 has been implicated in enhancing the defence response by influencing the redirection of secondary metabolic pathways [140].

Light-responsive miRNAs in *Solanum tuberosum* play a crucial role in overseeing lipid biosynthesis, alkaloid metabolism, and cellulose catabolism, as highlighted in a study by Qiao *et al.* [141]. When subjected to cadmium-induced stress, *Brassica napus* exhibited specific miRNA activity associated with governing the biotic stress response, controlling transcription factors, and modulating the synthesis of secondary metabolites [142]. Transcription factors ARF1 and ARF9 have been identified as drivers of camalexin biogenesis, leading to a robust defensive reaction against *Alternaria brassicicola*, a necrotrophic fungus, as evidenced in another study by Nafisi *et al*. [143]. Moreover, these transcription factors serve to inhibit the accumulation of glucosinolates, compounds that have a detrimental impact on a broad spectrum of bacteria [144].

Within *Arabidopsis* plants, the regulatory role of miR858a extends to the modulation of multiple MYB transcription factors. These MYB transcription factors hold significance in orchestrating the intricacies of the flavonoid biosynthesis pathway. When miR858a is overexpressed, it exerts a downregulatory influence on MYB transcription factors. This impact becomes evident through the manipulation of miR858 target mimic (MIM858 lines), where interference with the mimic leads to heightened expression levels of MYBs. This, in turn, results in a redirection of the metabolic flow, favouring an increased emphasis on the synthesis of flavonoids [145]. As a consequence, plants displaying elevated miR858 levels become more vulnerable to fungal infections. Conversely, plants possessing MIM858 lines exhibit resistance to pathogenic invasions, as demonstrated in reference [146]. In the context of *Withania somnifera*, distinct miRNAs such as miR477 and miR530 within leaf tissue, and miR159 and miR5140 within root tissue, assume regulatory roles in governing the production of secondary metabolites [146]. Furthermore, in subcultured Taxus cells, both miR8154 and

miR5298b have been identified as contributors to the augmentation of flavonoid and phenylpropanoid synthesis [147].

ENVIRONMENTAL STRESS RESPONSES

Jones-Rhoades and Bartel proposed that, under sulfate-depleted conditions in *Arabidopsis* plants, the levels of miR395 are elevated [148]. This discovery indicates that miRNA production is influenced not solely by developmental cues but also by external environmental factors. The target of miR395 is the ATP sulfurylase APS4 enzyme, which plays a role in the assimilation of inorganic sulfates and exhibits increased accumulation under conditions of low sulfur availability [149]. miR393 and miR319c exhibited heightened expression levels upon exposure to various stressors, while the expression of miR389a, miR397b, and miR402 decreased under stress-inducing conditions such as cold, dehydration, salinity, and abscisic acid (ABA) treatment [150]. These specific miRNAs are triggered in response to environmental stress conditions and play a role in enhancing the plant's protective mechanisms, contributing to its structural and mechanical resilience [151]. Furthermore, both gibberellic acid (GA) and abscisic acid (ABA) play a pivotal role in responding to diverse environmental stresses, as they regulate the expression of miR159. Additionally, these hormones exert control over the development of floral organs [152]. Recent investigations highlighting the influence of abiotic stress treatment on both the stress-tolerant 7B-1 tomato mutant and wild-type plants have revealed distinct miRNA expression profiles across various stress conditions. Specifically, miRNA159 exhibited decreased expression levels during cold, abscisic acid (ABA), and sodium chloride (NaCl) treatments. In contrast, miRNA166 displayed modified expression patterns in root and hypocotyl tissues. Similarly, miR159, miR472, and miR482 demonstrated opposite expression patterns between hypocotyl and root tissues [153].

Symbiosis

The decrease in disease resistance gene expression and increase in levels of legume-specific miRNAs targeting them (e.g., miR5213, miR5281) were observed during AM symbiosis in *Medicago truncatula* [154]. Also, miR482 targets NBS-LRR transcripts reported to be induced during establishment of symbiosis between soybean and *Bradyrhizobium japonicum* [155]. It was upregulated following PVY infection in the tolerant potato-PVY interaction. Many miRNAs regulate rhizobial and AM symbioses, which are implicated in the direct or indirect regulation of auxin signalling genes [154, 156]. Interestingly, many miRNAs, namely miR160, miR164, miR167, miR390, and miR393 were found to be similarly regulated during tolerance response of potato to PVY. Also, decreased GA levels were shown to be regulated by a miRNA/phasiRNA circuit in the potato tolerance response [157] and to be involved in rhizobial and mycorrhizal signalling networks [157–159]. miR169, miR171 and miR319, were upregulated in tolerant response to PVY in potato, such as also regulate nodulation and AM symbiosis in different legume species [154, 160]. miR171 was linked to tolerance in several viral pathosystems [161–163]. Rice overexpressing miR171 is less susceptible to RSV and shows attenuated disease symptoms, whereas reducing miR171 accumulation leads to development of disease symptoms [163].

Reproduction

Heterochromatic siRNAs primarily function to uphold genome stability by suppressing repetitive sequences and transposable elements. However, these siRNAs are not recognized for their involvement in developmental processes. Mutant strains of *Arabidopsis* that substantially diminish heterochromatic siRNA activity do not display evident developmental abnormalities. Recent studies have found plant siRNAs' role in germline specification and gamete formation.

In contrast to animals, which establish a germline early in embryogenesis, plants determine their germ line later in development within both their female and male reproductive structures. In *Arabidopsis*, within numerous developing ovules, a single cell located in the subepidermal layer differentiates into the female archespore, also referred to as the megaspore mother cell (MMC), marking the initiation of the female germ line. The MMC undergoes meiosis to yield four spores, with one of these spores undergoing three consecutive rounds of mitosis, ultimately giving rise to an eight-celled

female gametophyte. Within this structure, one of the cells develops into the egg. The absence of AGO9 function, a gene encoding a component of the AGO4-clade known for its interaction with heterochromatic siRNAs, leads to the formation of ovules containing multiple MMCs [164, 165].

In maize, the disruption of AGO4 function results in abnormalities related to the condensation and segregation of chromosomes during meiosis in the MMC [166]. Consequently, heterochromatic siRNAs likely play a crucial role in ensuring accurate female germline specification and the formation of gametes. In *Arabidopsis*, mutants with impaired ta-siRNA biogenesis, such as rdr6 and sgs3 mutants, display female germ line defects that bear resemblance to the defects observed in ago9 mutants [164]. Rice and maize have unveiled a fascinating category of phasiRNAs that exhibit significant accumulation within their flowers. Within this context, two conserved 22-nt miRNAs have been identified in both rice and maize, which initiate the generation of phasiRNAs originating from approximately 1000 distinct genomic loci in rice [167]. The phasiRNAs play a role in facilitating either germline specification or meiosis. Notably, a specific argonaute gene in rice called MEL1 exhibits expression exclusively within male and female archesporial cells. Disruption of MEL1 function in mel1 mutants results in observable defects during the process of meiosis [168].

CONCLUSION

Many miRNAs and certain siRNAs have long been known to impact developmental patterning in plants, whereas the role of sRNAs and their involvement in plant defence mechanisms are a result of recent studies. Small RNA regulation is complicated further by the miRNA-processing machinery, which allows the same miRNA to act differently in various tissues, for instance miR393, this single miRNA has different targets to play different roles such as in root development, vegetative shoot and leaf development, pathogen-triggered immunity (PTI), confer resistance against the bacterial pathogen *Pseudomonas syringae* pv. The tomato (Pto) DC3000 strain promotes the defence response by redirecting secondary metabolic flow.

REFERENCES

1. Baulcombe D. RNA silencing in plants. Nature. 2004; 431(7006): 356–363. [PubMed: 15372043]
2. Chapman EJ, Carrington JC. Specialisation and evolution of endogenous small RNA pathways. Nat Rev Genet. 2007; 8(11): 884–896.
3. Vaucheret H. Post-transcriptional small RNA pathways in plants: mechanisms and regulations. Genes Dev. 2006; 20(7): 759–771. [PubMed: 16600909]
4. Vazquez F. Arabidopsis endogenous small RNAs: highways and byways. Trends Plant Sci. 2006; 11(9): 460–468. [PubMed: 16893673]
5. Axtell MJ. Classification and comparison of small RNAs from plants. Annu Rev Plant Biol. 2013; 64: 137–159.
6. Hutvagner G, Simard MJ. Argonaute proteins: key players in RNA silencing. Nat Rev Mol Cell Biol. 2008; 9(1): 22–32. [PubMed: 18073770]
7. Katiyar-Agarwal S, Gao S, Vivian-Smith A, Jin H. A novel class of bacteria-induced small RNAs in Arabidopsis. Genes Dev. 2007; 21(23): 3123–3134. [PubMed: 18003861]
8. Katiyar-Agarwal S, Morgan R, Dahlbeck D, Borsani O, Villegas A Jr, *et al*. A pathogen-inducible endogenous siRNA in plant immunity. Proc Natl Acad Sci USA. 2006; 103(47): 18002–18007. [PubMed: 17071740]
9. Chen X. Small RNAs and their roles in plant development. Annu Rev Cell Dev Biol. 2009; 25: 21–44.
10. Lim LP, Lau NC, Weinstein EG, Abdelhakim A, Yekta S, Rhoades MW, Burge CB, Bartel DP. The microRNAs of *Caenorhabditis elegans*. Genes Dev. 2003; 17(8): 991–1008.
11. Molnar A, Schwach F, Studholme DJ, Thuenemann EC, Baulcombe DC. miRNAs control gene expression in the single-cell alga *Chlamydomonas reinhardtii*. Nature. 2007; 447(7148): 1126–1129.

12. Zhao X, Zhang H, Li L. Identification and analysis of the proximal promoters of microRNA genes in Arabidopsis. Genomics. 2013; 101(3): 187–194.
13. Barik S, SarkarDas S, Singh A, Gautam V, Kumar P, Majee M, Sarkar AK. Phylogenetic analysis reveals conservation and diversification of microRNA166 genes among diverse plant species. Genomics. 2014; 103(1): 114–121.
14. Vazquez F, Gasciolli V, Crete P, Vaucheret H. The nuclear dsRNA binding protein HYL1 is required for microRNA accumulation and plant development, but not posttranscriptional transgene silencing. Curr Biol. 2004; 14(4): 346–351.
15. Yu B, Yang Z, Li J, Minakhina S, Yang M, Padgett RW, Steward R, Chen X. Methylation as a crucial step in plant microRNA biogenesis. Science. 2005; 307(5711): 932–935.
16. Huang J, Yang M, Zhang X. The function of small RNAs in plant biotic stress response. J Integr Plant Biol. 2016; 58(4): 312–327.
17. Huang J, Yang M, Lu L, Zhang X. Diverse functions of small RNAs in different plant–pathogen communications. Front Microbiol. 2016; 7: 1552.
18. Petricka JJ, Winter CM, Benfey PN. Control of Arabidopsis root development. Annu Rev Plant Biol. 2012; 63: 563–590.
19. Wang JW, Wang LJ, Mao YB, Cai WJ, Xue HW, Chen XY. Control of root cap formation by MicroRNA-targeted auxin response factors in Arabidopsis. Plant Cell. 2005; 17(8): 2204–2216.
20. Mallory AC, Bartel DP, Bartel B. MicroRNA-directed regulation of Arabidopsis AUXIN RESPONSE FACTOR17 is essential for proper development and modulates expression of early auxin response genes. Plant Cell. 2005; 17(5): 1360–1375.
21. Gutierrez L, Bussell JD, Pacurar DI, Schwambach J, Pacurar M, Bellini C. Phenotypic plasticity of adventitious rooting in Arabidopsis is controlled by complex regulation of AUXIN RESPONSE FACTOR transcripts and microRNA abundance. Plant Cell. 2009; 21(10): 3119–3132.
22. Sorin C, Bussell JD, Camus I, *et al*. Auxin and light control of adventitious rooting in Arabidopsis require ARGONAUTE1. Plant Cell. 2005; 17(5): 1343–1359.
23. Guo HS, Xie Q, Fei JF, Chua NH. MicroRNA directs mRNA cleavage of the transcription factor NAC1 to downregulate auxin signals for arabidopsis lateral root development. Plant Cell. 2005, 17(5): 1376–1386.
24. Carlsbecker A, Lee JY, Roberts CJ, Dettmer J, Lehesranta S, ZhouJ, Lindgren O, Moreno-Risueno MA, Vaten A, Thitamadee S, Campilho A, Sebastian J, Bowman JL, Helariutta Y, Benfey PN. Cell signalling by microRNA165/6 directs gene dosedependent root cell fate. Nature. 2010; 465(7296): 316–321.
25. Singh A, Roy S, Singh S, Das SS, Gautam V, Yadav S, Kumar A, Singh A, Samantha S, Sarkar AK. Phytohormonal crosstalk modulates the expression of miR166/165s, target Class III HD-ZIPs, and KANADI genes during root growth in Arabidopsis thaliana. Sci Rep. 2017; 7(1): 3408.
26. Bazin J, Khan GA, Combier JP, *et al*. miR396 affects mycorrhization and root meristem activity in the legume Medicago truncatula. Plant J. 2013; 74(6): 920–934.
27. Rodriguez RE, Ercoli MF, Debernardi JM, Breakfield NW, Mecchia MA, Sabatini M, Cools T, De Veylder L, Benfey PN, Palatnik JF. MicroRNA miR396 regulates the switch between stem cells and transit-amplifying cells in Arabidopsis roots. Plant Cell. 2015; 27(12): 3354–3366.
28. Dolan L, Janmaat K, Willemsen V, Linstead P, Poethig S, Roberts K, Scheres B. Cellular organisation of the Arabidopsis thaliana root. Development. 1993; 119(1): 71–84.
29. Wang L, Mai YX, Zhang YC, Luo Q, Yang HQ. Micro-RNA171c-targeted SCL6-II, SCL6-III, and SCL6-IV genes regulate shoot branching in Arabidopsis. Mol Plant. 2010; 3(5): 794–806.
30. Lauressergues D, Delaux PM, Formey D, Lelandais-Briere C, Fort S, Cottaz S, Becard G, Niebel A, Roux C, Combier JP. The microRNA miR171h modulates arbuscular mycorrhizal colonisation of Medicago truncatula by targeting NSP2. Plant J. 2012; 72(3): 512–522.
31. Zhou Y, Liu X, Engstrom EM, Nimchuk ZL, Pruneda-Paz JL, Tarr PT, Yan A, Kay SA, Meyerowitz EM. Control of plant stem cell function by conserved interacting transcriptional regulators. Nature. 2015; 517(7534): 377–380.

32. Wang JJ, Guo HS. Cleavage of INDOLE-3-ACETIC ACID INDUCIBLE28 mRNA by microRNA847 upregulates auxin signalling to modulate cell proliferation and lateral organ growth in Arabidopsis. Plant Cell. 2015; 27(3): 574–590.
33. Liu Z, Kumari S, Zhang L, Zheng Y, Ware D. Characterization of miRNAs in response to short-term waterlogging in three inbred lines of Zea mays. PLoS ONE. 2012; 7(6): e39786.
34. Xie Q, Frugis G, Colgan D, Chua NH. Arabidopsis NAC1 transduces auxin signal downstream of TIR1 to promote lateral root development. Genes Dev. 2000; 14(23): 3024–3036.
35. Chen ZH, Bao ML, Sun YZ, Yang YJ, Xu XH, Wang JH, Han N, Bian HW, Zhu MY. Regulation of auxin response by miR393-targeted transport inhibitor response protein 1 is involved in normal development in Arabidopsis. Plant Mol Biol. 2011; 77(6): 619–629.
36. Bian H, Xie Y, Guo F, Han N, Ma S, Zeng Z, Wang J, Yang Y, Zhu M. Distinctive expression patterns and roles of the miRNA393/TIR1 homolog module in regulating flag leaf inclination and primary and crown root growth in rice (Oryza sativa). New Phytol. 2012; 196(1): 149–161.
37. Marin E, Jouannet V, Herz A, Lokerse AS, Weijers D, Vaucheret H, Nussaume L, Crespi MD, Maizel A. miR390, Arabidopsis TAS3 tasiRNAs, and their AUXIN RESPONSE FACTOR targets define an autoregulatory network quantitatively regulating lateral root growth. Plant Cell. 2010; 22(4): 1104–1117.
38. Yoon EK, Yang JH, Lim J, Kim SH, Kim SK, Lee WS. Auxin regulation of the microRNA390-dependent transacting small interfering RNA pathway in Arabidopsis lateral root development. Nucleic Acids Res. 2010; 38(4): 1382–1391.
39. Barton MK. Twenty years on: the inner workings of the shoot apical meristem, a developmental dynamo. Dev Biol. 2010; 341(1): 95–113.
40. McConnell JR, Barton MK. Leaf polarity and meristem formation in Arabidopsis. Development. 1998; 125(15): 2935–2942.
41. McConnell JR, Barton MK. Effect of mutations in the PINHEAD gene of Arabidopsis on the formation of shoot apical meristems. Dev Genet. 1995; 16(4): 358–366.
42. Ji L, Liu X, Yan J, Wang W, Yumul RE, Kim YJ, Dinh TT, Liu J, Cui X, Zheng B. *et al*. ARGONAUTE10 and ARGONAUTE1 regulate the termination of floral stem cells through two microRNAs in Arabidopsis. PLoS Genet. 2011; 7(3): e1001358.
43. Liu Q, Yao X, Pi L, Wang H, Cui X, Huang H. The ARGONAUTE10 gene modulates shoot apical meristem maintenance and establishment of leaf polarity by repressing miR165/166 in Arabidopsis. Plant J. 2009; 58(1): 27–40.
44. Zhu H, Hu F, Wang R, Zhou X, Sze SH, Liou LW, Barefoot A, Dickman M, Zhang X. Arabidopsis ARGONAUTE10 specifically sequesters miR166/165 to regulate shoot apical meristem development. Cell. 2011; 145(2): 242–256.
45. Zhou Y, Honda M, Zhu H, Zhang Z, Guo X, Li T, Li Z, Peng X, Nakajima K, Duan L, *et al*. Spatiotemporal sequestration of miR165/166 by Arabidopsis ARGONAUTE10 promotes shoot apical meristem maintenance. Cell Rep. 2015; 10(11): 1819–1827.
46. Schoof H, Lenhard M, Haecker A, Mayer KFX, Jurgens G, Laux T. The stem cell population of Arabidopsis shoot meristems is maintained by a regulatory loop between the CLAVATA and WUSCHEL genes. Cell. 2000; 100(6): 635–644.
47. Javelle M, Timmermans MC, Tucker MR, Laux T. A protodermal miR394 signal defines a region of stem cell competence in the Arabidopsis shoot meristem. Dev Cell. 2013; 24(2): 125–132.
48. Si-Ammour A, Windels D, Arn-Bouldoires E, Kutter C, Ailhas J, Meins F Jr, Vazquez F. miR393 and secondary siRNAs regulate expression of the TIR1/AFB2 auxin receptor clade and auxin related development of Arabidopsis leaves. Plant Physiol. 2011; 157(2): 683–691.
49. Xia K, Wang R, Ou X, Fang Z, Tian C, Duan J, Wang Y, Zhang M. OsTIR1 and OsAFB2 downregulation via OsmiR393 overexpression leads to more tillers, early flowering and less tolerance to salt and drought in rice. PLoS One. 2012; 7(1): e30039.
50. Rodriguez RE, Mecchia MA, Debernardi JM, Schommer C, Weigel D, Palatnik JF. Control of cell proliferation in Arabidopsis thaliana by microRNA miR396. Development. 2010; 137(1): 103–112.

51. Liu DM, Song Y, Chen ZX, Yu DQ. Ectopic expression of miR396 suppresses GRF target gene expression and alters leaf growth in Arabidopsis. Physiol Plant. 2009; 136(2): 223–236.
52. Wang L, Gu XL, Xu DY, Wang W, Wang H, Zeng MH, Chang ZY, Huang H, Cui XF. miR396-targeted AtGRF transcription factors are required for coordination of cell division and differentiation during leaf development in Arabidopsis. J Exp Bot. 2011; 62(2): 761–773.
53. Debernardi JM, Mecchia MA, Vercruyssen L, Smaczniak C, Kaufmann K, Inze D, Rodriguez RE, Palatnik JF. Posttranscriptional control of GRF transcription factors by microRNA miR396 and GIF co-activator affects leaf size and longevity. Plant J. 2014; 79(3): 413–426.
54. Aida M, Ishida T, Tasaka M. Shoot apical meristem and cotyledon formation during Arabidopsis embryogenesis: interaction among the CUP-SHAPED COTYLEDON and SHOOT MERISTEMLESS genes. Development. 1999; 126(8): 1563–1570.
55. Aida M, Ishida T, Fukaki H, Fujisawa H, Tasaka M. Genes involved in organ separation in Arabidopsis: an analysis of the cup shaped cotyledon mutant. Plant Cell. 1997; 9(6): 841–857.
56. Laufs P, Peaucelle A, Morin H, Traas J. MicroRNA regulation of the CUC genes is required for boundary size control in Arabidopsis meristems. Development. 2004; 131(17): 4311–4322.
57. Mallory AC, Dugas DV, Bartel DP, Bartel B. MicroRNA regulation of NAC-domain targets is required for proper formation and separation of adjacent embryonic, vegetative, and floral organs. Curr Biol. 2004; 14(12): 1035–1046.
58. Sieber P, Wellmer F, Ghyselinck J, Riechmann JL, Meyerowitz EM. Redundancy and specialisation among plant microRNAs: role of the MIR164 family in developmental robustness. Development. 2007; 134(6): 1051–1060.
59. Yu N, Cai WJ, Wang S, Shan CM, Wang LJ, Chen XY. Temporal control of trichome distribution by microRNA156-targeted SPL genes in Arabidopsis thaliana. Plant Cell. 2010; 22(7): 2322–2335.
60. Shikata M, Koyama T, Mitsuda N, Ohme-Takagi M. Arabidopsis SBP-box genes SPL10 SPL11 and SPL2 control morphological change in association with shoot maturation in the reproductive phase. Plant Cell Physiol. 2009; 50(12): 2133–2145.
61. Yamaguchi A, Wu MF, Yang L, Wu G, Poethig RS, Wagner D. The microRNA-regulated SBP-Box transcription factor SPL3 is a direct upstream activator of LEAFY FRUITFUL, and APETALA1. Dev Cell. 2009; 17(2): 268–278.
62. Wang JW, Czech B, Weigel D. miR156-regulated SPL transcription factors define an endogenous flowering pathway in Arabidopsis thaliana. Cell. 2009; 138(4): 738–749.
63. Yu ZX, Wang LJ, Zhao B, Shan CM, Zhang YH, Chen DF, Chen XY. Progressive regulation of sesquiterpene biosynthesis in Arabidopsis and Patchouli (Pogostemon cablin) by the miR156-targeted SPL transcription factors. Mol Plant. 2015; 8(1): 98–110.
64. Gou JY, Felippes FF, Liu CJ, Weigel D, Wang JW. Negative regulation of anthocyanin biosynthesis in Arabidopsis by a miR156-targeted SPL transcription factor. Plant Cell. 2011; 23(4): 1512–1522.
65. Stief A, Altmann S, Hoffmann K, Pant BD, Scheible WR, Baurle I. Arabidopsis miR156 regulates tolerance to recurring environmental stress through SPL transcription factors. Plant Cell. 2014; 26(4): 1792–1807.
66. Cui LG, Shan JX, Shi M, Gao JP, Lin HX. The miR156-SPL9-DFR pathway coordinates the relationship between development and abiotic stress tolerance in plants. Plant J. 2014; 80(6): 1108–1117.
67. Bergonzi S, Albani MC, Ver Loren van Themaat E, Nordstrom KJ, Wang R, Schneeberger K, Moerland PD, Coupland G. Mechanisms of age-dependent response to winter temperature in perennial flowering of Arabis alpina. Science. 2013; 340(6136): 1094–1097.
68. Zhou CM, Zhang TQ, Wang X, Yu S, Lian H, Tang H, Feng ZY, Zozomova-Lihova J, Wang JW. Molecular basis of age dependent vernalization in Cardamine flexuosa. Science. 2013; 340(6136): 1097–1100.
69. Schwarz S, Grande AV, Bujdoso N, Saedler H, Huijser P. The microRNA regulated SBP-box genes SPL9 and SPL15 control shoot maturation in Arabidopsis. Plant Mol Biol. 2008; 67(1–2): 183–195.
70. Wu G, Park MY, Conway SR, Wang JW, Weigel D, Poethig RS. The sequential action of miR156 and miR172 regulates developmental timing in Arabidopsis. Cell. 2009; 138(4): 750–759.

71. Yant L, Mathieu J, Dinh TT, Ott F, Lanz C, Wollmann H, Chen XM, Schmid M. Orchestration of the floral transition and floral development in Arabidopsis by the bifunctional transcription factor APETALA2. Plant Cell. 2010; 22(7): 2156–2170.
72. Shleizer-Burko S, Burko Y, Ben-Herzel O, Ori N. Dynamic growth program regulated by LANCEOLATE enables flexible leaf patterning. Development. 2011; 138(4): 695–704.
73. Zhou M, Li D, Li Z, Hu Q, Yang C, Zhu L, Luo H. Constitutive expression of a miR319 gene alters plant development and enhances salt and drought tolerance in transgenic creeping bentgrass. Plant Physiol. 2013; 161(3): 1375–1380.
74. Mao Y, Wu F, Yu X, Bai J, Zhong W, He Y. MicroRNA319atargeted Brassica rapa ssp. pekinensis TCP genes modulate head shape in Chinese cabbage by differential cell division arrest in leaf regions. Plant Physiol. 2014; 164(2): 710–720.
75. Efroni I, Blum E, Goldschmidt A, Eshed Y. A protracted and dynamic maturation schedule underlies Arabidopsis leaf development. Plant Cell. 2008; 20(9): 2293–2306.
76. Palatnik JF, Allen E, Wu XL, Schommer C, Schwab R, Carrington JC, Weigel D. Control of leaf morphogenesis by microRNAs. Nature. 2003; 425(6955): 257–263.
77. Ori N, Cohen AR, Etzioni A, Brand A, Yanai O, Schleizer S, Menda N, Amsellem Z, Efroni I, Pekker I, *et al*. Regulation of LANCEOLATE by miR319 is required for compound-leaf development in tomato. Nat Genet. 2007; 39(6): 787–791.
78. Koyama T, Mitsuda N, Seki M, Shinozaki K, Ohme-Takagi M. TCP transcription factors regulate the activities of ASYMMETRIC LEAVES1 and miR164, as well as the auxin response, during differentiation of leaves in Arabidopsis. Plant Cell. 2010; 22(11): 3574–3588.
79. Schommer C, Debernardi JM, Bresso EG, Rodriguez RE, Palatnik JF. Repression of cell proliferation by miR319regulated TCP4. Mol Plant. 2014; 7(10): 1533–1544.
80. Efroni I, Han SK, Kim HJ, Wu MF, Steiner E, Birnbaum KD, Hong JC, Eshed Y, Wagner D. Regulation of leaf maturation by chromatin-mediated modulation of cytokinin responses. Dev Cell. 2013; 24(4): 438–445.
81. Yanai O, Shani E, Russ D, Ori N. Gibberellin partly mediates LANCEOLATE activity in tomatoes. Plant J. 2011; 68(4): 571–582.
82. Koyama T, Furutani M, Tasaka M, Ohme-Takagi M. TCP transcription factors control the morphology of shoot lateral organs via negative regulation of the expression of boundary specific genes in Arabidopsis. Plant Cell. 2007; 19(2): 473–484.
83. Alonso-Peral MM, Li J, Li Y, Allen RS, Schnippenkoetter W, Ohms S, White RG, Millar AA. The microRNA159-regulated GAMYB-like genes inhibit growth and promote programmed cell death in Arabidopsis. Plant Physiol. 2010; 154(2): 757–771.
84. Ellis CM, Nagpal P, Young JC, Hagen G, Guilfoyle TJ, Reed JW. AUXIN RESPONSE FACTOR1 and AUXIN RESPONSE FACTOR2 regulate senescence and floral organ abscission in Arabidopsis thaliana. Development. 2005; 132(20): 4563–4574.
85. Lim PO, Lee IC, Kim J, Kim HJ, Ryu JS, Woo HR, Nam HG. AUXIN RESPONSE FACTOR2 (ARF2) plays a major role in regulating auxin-mediated leaf longevity. J Exp Bot. 2010; 61(5): 1419–1430.
86. Willmann MR, Endres MW, Cook RT, Gregory BD. The functions of RNA-dependent RNA polymerases in Arabidopsis. Arabidopsis Book. 2011; 9: e0146.
87. Das SS, Karmakar P, Nandi AK, Sanan-Mishra N. Small RNA mediated regulation of seed germination. Front Plant Sci. 2015; 6: 828.
88. Liu PP, Montgomery TA, Fahlgren N, Kasschau KD, Nonogaki H, Carrington JC. Repression of AUXIN RESPONSE FACTOR10 by microRNA160 is critical for seed germination and post-germination stages. Plant J. 2007; 52(1): 133–146.
89. Kim JY, Kwak KJ, Jung HJ, Lee HJ, Kang H. MicroRNA402 affects seed germination of *Arabidopsis thaliana* under stress conditions via targeting DEMETER-LIKE Protein3 mRNA. Plant Cell Physiol. 2010; 51(6): 1079–1083.
90. Jung HJ, Kang H. Expression and functional analyses of micro-RNA417 in Arabidopsis thaliana under stress conditions. Plant Physiol Biochem. 2007; 45(10–11): 805–811.

91. Kim JY, Lee HJ, Jung HJ, Maruyama K, Suzuki N, Kang H. Overexpression of microRNA395c or 395e affects the seed germination of *Arabidopsis thaliana* under stress conditions. Planta. 2007; 232(6): 1447–1454.
92. Wang S, Wu K, Yuan Q, *et al*. Control of grain size, shape and quality by OsSPL16 in rice. Nat Genet. 2012; 44(8): 950–954.
93. Wang S, Li S, Liu Q, *et al*. The OsSPL16-GW7 regulatory module determines grain shape and simultaneously improves rice yield and grain quality. Nat Genet. 2015; 47(8): 949–954.
94. Duan P, Ni S, Wang J, Zhang B, Xu R, Wang Y, Chen H, Zhu X, Li Y. Regulation of OsGRF4 by OsmiR396 controls grain size and yield in rice. Nat Plants. 2015; 2: 15203.
95. Yan J, Zhao C, Zhou J, Yang Y, Wang P, Zhu X, Tang G, Bressan RA, Zhu JK. The miR165/166 mediated regulatory module plays critical roles in ABA homeostasis and response in *Arabidopsis thaliana*. PLoS Genet. 2016; 12(11): e1006416.
96. Li C, Zhang B. MicroRNAs in control of plant development. J Cell Physiol. 2016 Feb; 231(2): 303–13.
97. Martin RC, Liu PP, Goloviznina NA, Nonogaki H. microRNA, seeds, and Darwin diverse function of miRNA in seed biology and plant responses to stress. J Exp Bot. 2010; 61(9): 2229–2234.
98. Xing S, Salinas M, Garcia-Molina A, Hohmann S, Berntgen R, Huijser P. SPL8 and miR156-targeted SPL genes redundantly regulate Arabidopsis gynoecium differential patterning. Plant J. 2013; 5(4): 566–577.
99. Gandikota M, Birkenbihl RP, Hohmann S, Cardon GH, Saedler H, Huijser P. The miRNA156/157 recognition element in the 3′ UTR of the Arabidopsis SBP box gene SPL3 prevent early flowering by translational inhibition in seedlings. Plant J. 2007; 49(4): 683–693.
100. Blazquez MA, Green R, Nilsson O, Sussman MR, Weigel D. Gibberellins promote flowering of arabidopsis by activating the LEAFY promoter. Plant Cell. 1998; 10(5): 791–800.
101. Rhoades MW, Reinhart BJ, Lim LP, Burge CB, Bartel B, Bartel DP. Prediction of plant microRNA targets. Cell. 2002; 110(4): 513–520.
102. Nikovics K, Blein T, Peaucelle A, Ishida T, Morin H, Aida M, Laufs P. The balance between the MIR164A and CUC2 genes controls leaf margin serration in Arabidopsis. Plant Cell. 2006; 18(11): 2929–2945.
103. Chen X. A microRNA as a translational repressor of APETALA2 in Arabidopsis flower development. Science. 2004; 303(5666): 2022–2025.
104. Achard P, Herr A, Baulcombe DC, Harberd NP. Modulation of floral development by a gibberellin-regulated microRNA. Development. 2004; 131(14): 3357–3365.
105. Aukerman MJ, Sakai H. Regulation of flowering time and floral organ identity by a MicroRNA and its APETALA2-like target genes. Plant Cell. 2003; 15(11): 2730–2741.
106. Nagpal P, Ellis CM, Weber H, Ploense SE, Barkawi LS, Guilfoyle TJ, Hagen G, Alonso JM, Cohen JD, Farmer EE, Ecker JR, Reed JW. Auxin response factors ARF6 and ARF8 promote jasmonic acid production and flower maturation. Development. 2005; 132(18): 4107–4118.
107. Wu MF, Tian Q, Reed JW. Arabidopsis microRNA167 controls patterns of ARF6 and ARF8 expression, and regulates both female and male reproduction. Development. 2006; 133(21): 4211–4218.
108. Cartolano M, *et al*. A conserved microRNA module exerts homeotic control over Petunia hybrida and Antirrhinum majus floral organ identity. Nat Genet. 2007; 39(7): 901–905.
109. Hong RL, *et al*. Regulatory elements of the floral homeotic gene AGAMOUS identified by phylogenetic footprinting and shadowing. Plant Cell. 2003; 15(6): 1296–1309.
110. Wagner GJ, Wang E, Shepherd RW. New approaches for studying and exploiting an old protuberance, the plant trichome. Ann Bot. 2004; 93(1): 3–11.
111. Navarro L, Dunoyer P, Jay F, Arnold B, Dharmasiri N, Estelle M, Voinnet O, Jones JDG. A plant miRNA contributes to antibacterial resistance by repressing auxin signaling. Science. 2006; 312(5772): 436–439.
112. Pandey P, Srivastava PK, Pandey SP. Prediction of plant miRNA targets. In: Methods in Molecular Biology. New York, NY, USA: Humana Press; 2019; 99–107.

113. Li Y, Zhang Q, Zhang J, Wu L, Qi Y, Zhou J-M. Identification of MicroRNAs involved in pathogen-associated molecular pattern-triggered plant innate immunity. Plant Physiol. 2010; 152(4): 2222–2231.
114. Li Y, Lu Y-G, Shi Y, Wu L, Xu Y-J, Huang F, Guo X-Y, Zhang Y, Fan J, Zhao J-Q, *et al*. Multiple rice MicroRNAs are involved in immunity against the blast fungus magnaporthe oryzae. Plant Physiol. 2014; 164(2): 1077–1092.
115. Dunoyer P, Himber C, Voinnet O. Induction, suppression and requirement of RNA silencing pathways in virulent Agrobacterium tumefaciens infections. Nat Genet. 2006; 38(2): 258–263.
116. Curaba J, Singh MB, Bhalla PL. miRNAs in the crosstalk between phytohormone signalling pathways. J Exp Bot. 2014; 65(6): 1425–1438.
117. Jagadeeswaran G, Saini A, Sunkar R. Biotic and abiotic stress down-regulate miR398 expression in Arabidopsis. Planta. 2009; 229(4): 1009–1014.
118. Zhang W, Gao S, Zhou X, Chellappan P, Chen Z, Zhou X, Zhang X, Fromuth N, Coutino G, Coffey M, *et al*. Bacteria Responsive microRNAs regulate plant innate immunity by modulating plant hormone networks. Plant Mol Biol. 2010; 75(1–2): 93–105.
119. Lee HJ, Park YJ, Kwak KJ, Kim D, Park JH, Lim JY, Shin C, Yang K-Y, Kang H. MicroRNA844-guided downregulation of cytidine diphosphate diacylglycerol synthase3 (CDS3) mRNA Affects the response of arabidopsis thaliana to bacteria and fungi. Mol Plant Microbe Interact. 2015; 28(8): 892–900.
120. Gupta OP, Permar V, Koundal V, Singh UD, Praveen S. MicroRNA regulated defence responses in Triticum aestivum L. during Puccinia graminis f.sp. tritici infection. Mol Bio Rep. 2011; 39(2): 817–824.
121. Stergiopoulos I, Burg HAVD, Okmen B, Beenen HG, Van Liere S, Kema GHJ, De Wit PJGM. Tomato Cf resistance proteins mediate recognition of cognate homologous effectors from fungi pathogenic on dicots and monocots. Proc Natl Acad Sci USA. 2010; 107(16): 7610–7615.
122. Yi H, Richards EJ. A cluster of disease resistance genes in arabidopsis is coordinately regulated by transcriptional activation and RNA silencing. Plant Cell. 2007; 19(9): 2929–2939.
123. Li F, Pignatta D, Bendix C, Brunkard JO, Cohn MM, Tung J, Sun H, Kumar P, Baker B. MicroRNA regulation of plant innate immune receptors. Proc Natl Acad Sci USA. 2012; 109(5): 1790–1795.
124. Shivaprasad PV, Chen H-M, Patel K, Bond DM, Santos BA, Baulcombe DCA. MicroRNA superfamily regulates nucleotide binding site–leucine-rich repeats and other mRNAs. Plant Cell. 2012; 24(3): 859–874.
125. Zhai J, Jeong D-H, De Paoli E, Park S, Rosen BD, Li Y, González AJ, Yan Z, Kitto SL, Grusak MA, *et al*. MicroRNAs as master regulators of the plant NB-LRR defence gene family via the production of phased, trans-acting siRNAs. Genes Dev. 2011; 25(23): 2540–2553.
126. Ouyang S, Park G, Atamian HS, Han CS, Stajich JE, Kaloshian I, Borkovich KA. MicroRNAs suppress NB domain genes in tomato that confer resistance to fusarium oxysporum. PLOS Pathog. 2014; 10(10): e1004464.
127. Boccara M, Sarazin A, Thiébeauld O, Jay F, Voinnet O, Navarro L, Colot V. The arabidopsis miR472-RDR6 silencing pathway modulates PAMP- and effector-triggered immunity through the post-transcriptional control of disease resistance genes. PLOS Pathog. 2014; 10(1): e1003883.
128. Liu J, Cheng X, Liu D, Xu W, Wise R, Shen QH. The miR9863 family regulates distinct Mla alleles in barley to attenuate NLR receptor-triggered disease resistance and cell-death signalling. PLoS Genet. 2014; 10(12): e1004755.
129. Niu D, Lii YE, Chellappan P, Lei L, Peralta K, Jiang C, Guo J, Coaker G, Jin H. miRNA863-3p sequentially targets negative immune regulator ARLPKs and positive regulator SERRATE upon bacterial infection. Nat Commun. 2016; 7: 11324(13p).
130. Wang H, Jiao X, Kong X, Hamera S, Wu Y, Chen X, Fang R, Yan Y. A signalling cascade from miR444 to RDR1 in rice antiviral RNA silencing pathway. Plant Physiol. 2016; 170(4): 2365–2377.
131. Mandadi KK, Scholthof K-BG. Plant immune responses against viruses: how does a virus cause disease. Plant Cell. 2013; 25(5): 1489–1505.

132. Wu J, Yang R, Yang Z, Yao S, Zhao S, Wang Y, Li P, Song X, Jin L, Zhou T, *et al*. ROS accumulation and antiviral defence control by microRNA528 in rice. Nat Plants. 2017; 3: 16203(7p).
133. Li T, Li H, Zhang YX, Liu JY. Identification and analysis of seven H2O2-responsive miRNAs and 32 new miRNAs in the seedlings of rice (Oryza sativa L. ssp. indica). Nucleic Acids Res. 2011; 39(7): 2821–2833.
134. Pacheco R, Garcı´a-Marcos A, Barajas D, Martia´n˜ez J, Tenllado F. PVX–potyvirus synergistic infections differentially alter microRNA accumulation in Nicotiana benthamiana. Virus Res. 2012; 165(2): 231–235.
135. Yin H, Hong G, Li L, Zhang X, Kong Y, Sun Z, Li J, Chen J, He Y. MiR156/SPL9 regulates reactive oxygen species accumulation and immune response in Arabidopsis thaliana. Phytopathology. 2019; 109(4): 632–642.
136. Zhang C, Ding Z, Wu K, Yang L, Li Y, Yang Z, Shi S, Liu X, Zhao S, Yang Z, *et al*. Suppression of jasmonic acid-mediated defence by viral-inducible microRNA319 facilitates virus infection in rice. Mol Plant. 2016; 9(9): 1302–1314.
137. Bazzini AA, Hopp HE, Beachy RN, Asurmendi S. Infection and coaccumulation of tobacco mosaic virus proteins alter microRNA levels, correlating with symptom and plant development. Proc Natl Acad Sci USA. 2007; 104(29): 12157–12162.
138. Wang S, Cui W, Wu X, Yuan Q, Zhao J, Zheng H, Lu Y, Peng J, Lin L, Chen J, *et al*. Suppression of nbe-miR166h-p5 attenuates leaf yellowing symptoms of potato virus X on Nicotiana benthamiana and reduces virus accumulation. Mol Plant Pathol. 2018; 19(11): 2384–2396.
139. Yin Z, Murawska Z, Xie F, Pawełkowicz M, Michalak K, Zhang B, Lebecka R. MicroRNA response in potato virus Y infected tobacco shows strain-specificity depending on host and symptom severity. Virus Res. 2019; 260: 20–32.
140. Padhan JK, Kumar P, Sood H, Chauhan RS. Prospecting NGS-transcriptomes to assess regulation of miRNA-mediated secondary metabolites biosynthesis in Swertia chirayita, a medicinal herb of the North-Western Himalayas. Med Plants. 2016; 8(3): 219–228.
141. Qiao Y, Zhang J, Zhang J, Wang Z, Ran A, Guo H, Wang D, Zhang J. Integrated RNA-seq and sRNA-seq analysis reveals miRNA effects on secondary metabolism in Solanum tuberosum L. Mol Genet Genom. 2017; 292(1): 37–52.
142. Jian H, Yang B, Zhang A, Ma J-Q, Ding Y, Chen Z, Li J-N, Xu X, Liu L. Genome-wide identification of micrornas in response to cadmium stress in oilseed rape (Brassica napus L.) using high-throughput sequencing. Int J Mol Sci. 2018; 19(5): 1431.
143. Nafisi M, Goregaoker S, Botanga CJ, Glawischnig E, Olsen CE, Halkier BA, Glazebrook J. Arabidopsis cytochrome P450 monooxygenase 71A13 catalyzes the conversion of Indole-3-acetaldoxime in camalexin synthesis. Plant Cell. 2007; 19(6): 2039–2052.
144. Aires A, Mota VR, Saavedra MJ, Monteiro AA, Simões M, Rosa EAS, Bennett RN. Initial in vitro evaluations of the antibacterial activities of glucosinolate enzymatic hydrolysis products against plant pathogenic bacteria. J Appl Microbiol. 2009; 106(6): 2096–2105.
145. Camargo-Ramírez R, Val-Torregrosa B, San Segundo B. MiR858-mediated regulation of flavonoid-specific MYB transcription factor genes controls resistance to pathogen infection in Arabidopsis. Plant Cell Physiol. 2018; 59(1): 190–204.
146. Srivastava S, Singh R, Srivastava G, Sharma A. Comparative study of withanolide biosynthesis-related miRNAs in root and leaf tissues of withania somnifera. Appl Biochem Biotechnol. 2018; 185(4): 1145–1159.
147. Zhang M, Dong Y, Nie L, Lu M, Fu C, Yu LJ. High-throughput sequencing reveals miRNA effects on the primary and secondary production properties in long-term subcultured Taxus cells. Front Plant Sci. 2015; 6: 604.
148. Jones-Rhoades MW, Bartel DP. Computational identification of plant MicroRNAs and their targets, including a stress-induced miRNA. Mol Cell. 2004; 14(6): 787–799.
149. Ai Q, Liang G, Zhang H, Yu D. Control of sulphate concentration by miR395-targeted APS genes in Arabidopsis thaliana. Plant Divers. 2016; 38(2): 92–100.
150. Sunkar R, Zhu JK. Novel and stress regulated microRNAs and other small RNAs from Arabidopsis w inside box sign. Plant Cell. 2004; 16(8): 2001–2019.

151. Lu S, Sun Y-H, Shi R, Clark C, Li L, Chiang VL. Novel and mechanical stress-responsive microRNAs in populus trichocarpa that are absent from Arabidopsis. Plant Cell. 2005; 17(8): 2186–2203.
152. Waheed S, Zeng L. The critical role of miRNAs in regulation of flowering time and flower development. Genes. 2020; 11(3): 319.
153. Omidvar V, Mohorianu I, Dalmay T, Zheng Y, Fei Z, Pucci A, Mazzucato A, Večeřová V, Sedlářova M, Fellner M. Transcriptional regulation of male-sterility in 7B-1 male-sterile tomato mutant. PLoS One. 2017; 12(2): e0170715.
154. Devers EA, Branscheid A, May P, Krajinski F. Stars and symbiosis: microRNA- and microRNA*-mediated transcript cleavage involved in arbuscular mycorrhizal symbiosis. Plant Physiol. 2011; 156(4): 1990–2010.
155. Li H, Deng Y, Wu TL, Subramanian S, Yu O. Misexpression of miR482, miR1512, and miR1515 increases soybean nodulation. Plant Physiol. 2010; 153(4): 1759–1770.
156. Allen E, Xie Z, Gustafson AM, Carrington JC. MicroRNA-directed phasing during trans-acting siRNA biogenesis in plants. Cell. 2005; 121(2): 207–221.
157. 168Jin Y, Liu H, Luo D, Yu N, Dong W, Wang C, Zhang X, Dai H, Yang J, Wang E. DELLA proteins are common components of symbiotic rhizobial and mycorrhizal signalling pathways. Nat Commun. 2016; 7: 12433(14p).
158. Floss DS, Levy JG, Le´vesque-tremblay V, Pumplin N, Harrison MJ. DELLA proteins regulate arbuscule formation in arbuscular mycorrhizal symbiosis. Proc Natl Acad Sci USA (PNAS). 2013 Dec 17; 110(51): 5025–5034.
159. Fonouni-Farde C, Tan S, Baudin M, Brault M, Wen J, Mysore KS, Niebel A, Frugier F, Diet A. DELLA-mediated gibberellin signalling regulates Nod factor signalling and rhizobial infection. Nat Commun. 2016; 7: 12636(13p).
160. Lelandais-Brie`re C, Naya L, Sallet E, Calenge F, Frugier F, Hartmann C, Gouzy J, Crespi M. Genome-wide Medicago truncatula small RNA analysis revealed novel microRNAs and isoforms differentially regulated in roots and nodules. Plant Cell. 2009; 21(9): 2780–2796.
161. Naqvi AR, Haq QMR, Mukherjee SK. MicroRNA profiling of tomato leaf curl new delhi virus (tolcndv) infected tomato leaves indicates that deregulation of mir159/319 and mir172 might be linked with leaf curl disease. Virol J. 2010; 7: 281(16p).
162. Feng J, Wang Y, Lin R, Chen J. Altered expression of microRNAs and target mRNAs in tomato root and stem tissues upon different viral infections. J Phytopathol. 2013; 161(2): 107–119.
163. Tong A, Yuan Q, Wang S, Peng J, Lu Y, Zheng H, Lin L, Chen H, Gong Y, Chen J, *et al*. Altered accumulation of osa-miR171b contributes to rice stripe virus infection by regulating disease symptoms. J Exp Bot. 2017; 68(15): 4357–4367.
164. Havecker ER, Wallbridge LM, Hardcastle TJ, Bush MS, Kelly KA, Dunn RM, Schwach F, Doonan JH, Baulcombe DC. The Arabidopsis RNA-directed DNA methylation argonautes functionally diverge based on their expression and interaction with target loci. Plant Cell. 2010; 22(2): 321–334.
165. Olmedo-Monfil V, Duran-Figueroa N, Arteaga-Vazquez M, Demesa-Arevalo E, Autran D, Grimanelli D, Slotkin RK, Martienssen RA, Vielle-Calzada JP. Control of female gamete formation by a small RNA pathway in Arabidopsis. Nature. 2010; 464(7288): 628–632.
166. Singh M, Goel S, Meeley RB, Dantec C, Parrinello H, Michaud C, Leblanc O, Grimanelli D. Production of viable gametes without meiosis in maize deficient for an ARGONAUTE protein. Plant Cell. 2011; 23(2): 443–458.
167. Johnson C, Kasprzewska A, Tennessen K, Fernandes J, Nan GL, Walbot V, Sundaresan V, Vance V, Bowman LH. Clusters and superclusters of phased small RNAs in the developing inflorescence of rice. Genome Res. 2009 Aug; 19(8): 1429–1440.
168. Nonomura K, Morohoshi A, Nakano M, Eiguchi M, Miyao A, Hirochika H, Kurata N. A germ cell specific gene of the ARGONAUTE family is essential for the progression of premeiotic mitosis and meiosis during sporogenesis in rice. Plant Cell. 2007; 19(8): 2583–2594.

