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MicroRNAs as Master Regulators of Plant Development and Stress Adaptation

Review Article

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Abstract

MicroRNAs (miRNAs) are small (~20–24 nt), non-coding RNAs that serve as master regulators of gene expression in plants, playing pivotal roles in growth, development, and stress adaptation. This review systematically examines the molecular mechanisms of miRNA biogenesis, from transcription and processing to their integration into RNA-induced silencing complexes (RISCs). We highlight their spatiotemporal regulation of key developmental processes—including leaf morphogenesis, root architecture, phase transitions, and reproductive development—and their adaptive roles in abiotic (drought, salinity, nutrient deficiency) and biotic (pathogens, herbivores) stress responses. The evolutionary conservation of miRNA pathways across plant species underscores their functional significance, while emerging biotechnological applications, such as engineered miRNAs and CRISPR-based editing, offer innovative strategies for crop improvement. By synthesizing current advances and future perspectives (e.g., single-cell miRNAomics, synthetic networks, and cross-kingdom signaling), this review provides a comprehensive framework for understanding miRNA-mediated regulation in plants and its potential to address global agricultural challenges.

Keywords: MicroRNAs (miRNAs); miRNA biogenesis; Gene regulation; Plant development; Stress responses;Crop improvement;Evolutionary conservation; RNA interference (RNAi)

Abbreviations

miRNAs: MicroRNAs; RNAi: RNA interference; pri-miRNAs: Primary miRNAs; DCL: DICER-LIKE Protein; RISC: RNA-induced silencing complex; AGO: Argonaute; TFs: Transcription Factors; ceRNAs: Competing endogenous RNAs; HATs: Histone acetyltransferases; HMTs: Histone methyltransferases; PRC2: Polycomb Repressive Complex 2; ADARs: Adenosine deaminases; PTI: PAMP-triggered immunity; SA: Salicylic acid: JA: Jasmonic acid; RBPs: RNA-Binding Proteins; ARFs: AUXIN RESPONSE FACTORs; SPL: SQUAMOSA PROMOTER.

BINDING PROTEIN-LIKE

AP2: APETALA2; SAM:Shoot Apical Meristem; AM: Axillary Meristem; LCR: LEAF CURLING RESPONSIVENESS; WUS:WUSCHEL; CLV3:CLAVATA3; PR: Pathogenesis-Related.

Introduction

MicroRNAs (miRNAs) are small, non-coding RNA molecules that typically range from 20 to 24 nucleotides in length, and they play a pivotal role in the post-transcriptional regulation of gene expression in plants [1]. These highly conserved regulatory molecules function as critical modulators of cellular processes, exerting their influence through sequence-specific interactions with target messenger RNAs [2]. Since their initial discovery in the early 1990s, miRNAs have

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been recognized as master regulators that orchestrate a wide array of biological functions throughout a plant's life cycle. Their importance extends across multiple physiological and developmental stages, where they fine-tune gene expression networks with remarkable precision [3]. By binding to complementary target mRNAs with high specificity, miRNAs induce either transcript degradation through cleavage or translational repression through inhibition of protein synthesis, enabling precise spatial and temporal control over gene expression. This sophisticated regulatory mechanism operates at multiple levels, ensuring proper cellular function and organismal development. This fine-tuning mechanism is particularly crucial for plants as sessile organisms, allowing them to rapidly adjust their gene expression profiles in response to internal cues and external stimuli. The ability to modulate gene expression dynamically is essential for plants to adapt to constantly changing environmental conditions while simultaneously coordinating complex developmental transitions that determine their growth patterns and reproductive success [4-6].

The first miRNA, *lin-4*, was discovered in *Caenorhabditis elegans* in 1993, revealing a novel layer of gene regulation mediated by small RNAs. This groundbreaking finding challenged the conventional understanding of genetic regulation and opened new avenues in molecular biology. Subsequent research identified miRNAs in animals and later in plants, demonstrating their evolutionary conservation and functional significance. The discovery of the RNA interference (RNAi) pathway further elucidated the mechanisms by which small RNAs modulate gene expression, solidifying miRNAs as key players in genetic regulation across eukaryotes [7-10].

The first plant miRNA, *miR171*, was identified in *Arabidopsis thaliana* in 2002, marking a major milestone in plant molecular biology. Early studies revealed that plant miRNAs differ from their animal counterparts in their biogenesis, target specificity, and functional roles. Unlike animal miRNAs, which often exhibit partial complementarity to their targets, plant miRNAs typically bind with near-perfect complementarity, leading to mRNA cleavage rather than translational repression. The identification of conserved miRNA families across land plants highlighted their fundamental roles in development and stress responses. Advances in high-throughput sequencing and bioinformatics have since expanded the catalogue of known plant miRNAs, uncovering their extensive regulatory networks [11-14].

This review provides a comprehensive overview of plant miRNAs, beginning with their biogenesis and maturation processes. We then discuss their critical functions in plant growth and development, including their roles in shoot and root architecture, leaf morphogenesis, and reproductive transitions. Additionally, we examine how miRNAs mediate responses to abiotic and biotic stresses, enabling plants to withstand adverse conditions. Finally, we explore the evolutionary conservation of miRNAs across plant species and their emerging applications in biotechnology, where engineered miRNAs are being harnessed to enhance crop resilience and productivity. By integrating current knowledge on miRNA biology, this review underscores their significance in both fundamental plant science and agricultural innovation.

miRNA biogenesis in plants

Transcription of Primary miRNAs (pri-miRNAs)

In plants, miRNA biogenesis begins with the transcription of miRNA genes by RNA Polymerase II, producing long primary transcripts called pri-miRNAs(Figure 1). These pri-miRNAs contain stem-loop structures that are essential for subsequent processing. Like typical mRNAs, they are modified with a 5' cap and a 3' polyadenylated tail, ensuring stability and proper nuclear processing. The transcription of pri-miRNAs is tightly regulated, influenced by developmental and environmental cues. This step ensures that miRNA levels are finely tuned to meet cellular demands, laying the foundation for downstream processing [15-18].

Processing by DICER-LIKE (DCL) Proteins

The pri-miRNAs are cleaved in the nucleus by the DICER-LIKE1 (DCL1) protein complex, which generates precursor miRNAs (pre-miRNAs) with shorter stem-loop structures. DCL1 works in coordination with auxiliary proteins like HYL1 and SE to ensure accurate and efficient processing. HYL1 stabilizes the pri-miRNA-DCL1 interaction, while SE aids in recruiting processing machinery (Figure 1). The precise cleavage by DCL1 is crucial for producing functional miRNA duplexes. Defects in these proteins can lead to improper miRNA maturation, affecting plant growth and stress responses [16-22].

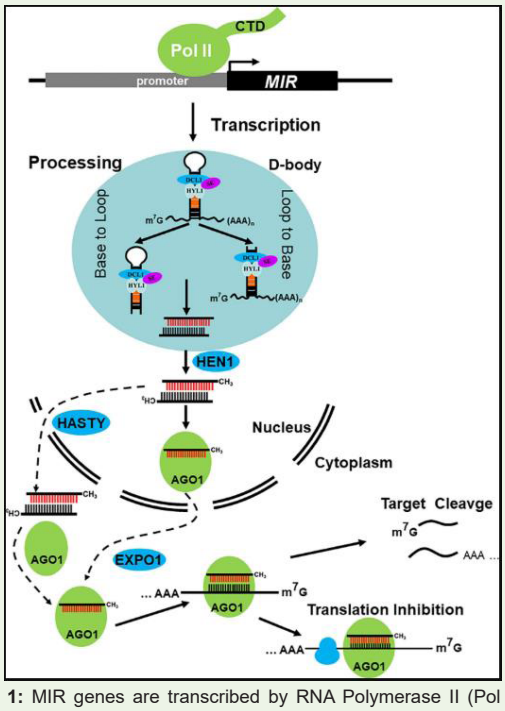

Figure 1: MIR genes are transcribed by RNA Polymerase II (Pol II) into primary miRNA transcripts (pri-miRNAs). These pri-miRNAs are processed into miRNA/miRNA* duplexes by the dicing complex in D-bodies, with cleavage occurring in either the base-to-loop or loop-to-base direction. The miRNA/miRNA* duplex is then methylated by the terminal methyltransferase HEN1 in the nucleus. The mature miRNA is loaded into AGO1 and exported via EXPO1, or the methylated duplex is transported to the cytoplasm via HASTY before being incorporated into AGO proteins for RNA silencing. Figure is adapted from Zhang et al. 2022 [16].

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Nuclear Export and Maturation

After processing, the miRNA duplex (miRNA:miRNA*) is exported to the cytoplasm by HASTY, the plant homolog of exportin-5. Once in the cytoplasm, the duplex is unwound, and the mature miRNA (guide strand) is loaded into the RNA-induced silencing complex (RISC). The passenger strand (miRNA*) is typically degraded, though some may also play regulatory roles. The incorporation of the miRNA into RISC marks the final step in maturation, enabling it to target complementary mRNAs for silencing. This selective export ensures only functional miRNAs mediate gene regulation [22-26].

Mode of Action: mRNA Silencing

Plant miRNAs primarily silence target mRNAs through cleavage, mediated by Argonaute (AGO) proteins, particularly AGO1. The miRNA-RISC complex binds near-perfect complementary sequences, leading to mRNA degradation. Some miRNAs also repress translation without cleavage, though this mechanism is less common in plants. miRNA-mediated silencing regulates diverse processes, including development, stress responses, and pathogen defense. The precision of this system highlights its importance in maintaining plant homeostasis and adaptability[27-31]

Regulation of miRNA biogenesis

Transcription Factors (TFs)

Specific TFs, such as MYB, WRKY, and bZIP families, bind to MIR gene promoters, either activating or repressing their transcription in a tissue-specific or stress-dependent manner. For example, in Arabidopsis, WRKY TFs modulate miRNA expression during pathogen defense, while MYB factors regulate developmental miRNAs. Some TFs act as master regulators, integrating hormonal and environmental signals to control miRNA production. Additionally, competing endogenous RNAs (ceRNAs) can sequester TFs, indirectly influencing MIR gene expression [32-34].

Epigenetic Modifications

Chromatin structure profoundly impacts MIR gene expression, with histone acetyltransferases (HATs) and methyltransferases (HMTs) dynamically modifying nucleosome positioning. DNA methylation at CpG islands, mediated by MET1 and DRM2, can silence MIR loci, whereas demethylation activates them. In plants, Polycomb Repressive Complex 2 (PRC2) deposits H3K27me3 marks to suppress certain MIR genes, while trithorax-group proteins promote activation via H3K4me3. Environmental stresses, such as cold or drought, can rapidly alter these epigenetic marks, reprogramming miRNA expression [35-38].

Drosha/DCL1 Complex: Post-Transcriptional Processing

In animals, the microprocessor complex (Drosha-DGCR8) recognizes and cleaves pri-miRNAs in the nucleus, whereas plants use DCL1 in association with HYL1 and SERRATE for precise processing. Structural features such as stem-loop stability and flanking sequences determine cleavage efficiency. Mutations in these core proteins lead to defective miRNA biogenesis, underscoring their essential role. Auxiliary factors like TOUGH and DAWDLE further enhance processing accuracy, ensuring proper miRNA maturation [39-42].

RNA Editing (ADAR/ADATs): Post-Transcriptional Processing

Adenosine deaminases (ADARs) convert adenosine (A) to inosine (I) in pri-miRNAs, altering their secondary structure and potentially blocking Dicer cleavage. Similarly, cytidine deaminases (e.g., APOBEC) induce C-to-U edits, which can disrupt miRNA-mRNA target pairing. These modifications are particularly prevalent in neural and immune tissues, adding another layer of regulatory complexity. In plants, RNA editing is less common but still influences miRNA function under stress conditions [43-47].

Alternative Splicing: Post-Transcriptional Processing

Some MIR genes contain introns that undergo alternative splicing, generating multiple pri-miRNA isoforms with distinct hairpin structures. This can lead to the production of different mature miRNAs from the same locus, expanding regulatory diversity. For instance, splicing variants of MIR172 in Arabidopsis produce functionally distinct miRNAs that regulate flowering time. Dysregulation of splicing factors (e.g., SR proteins) can thus have cascading effects on miRNA-mediated gene silencing [48-51].

Abiotic Stress Responses

Drought, extreme temperatures, and nutrient deficiencies trigger kinase cascades (e.g., SnRK2, MAPKs) that phosphorylate miRNA-processing machinery, modulating their activity. For example, osmotic stress induces SnRK2-mediated phosphorylation of DCL1, enhancing miRNA production to suppress growth-related genes. Heavy metals like cadmium can upregulate specific miRNAs (e.g., miR398) to activate detoxification pathways, illustrating adaptive miRNA regulation [51-55].

Biotic Stress Responses

Pathogen infection activates immune signaling through PAMP-triggered immunity (PTI), leading to miRNA reprogramming. Salicylic acid (SA) and jasmonic acid (JA) pathways induce miRNAs (e.g., miR393, miR160) that silence negative regulators of defense responses. Viral suppressors of RNA silencing (VSRs) often target DCL1 or AGO1 to block host miRNA biogenesis, highlighting the evolutionary arms race between pathogens and host miRNA machinery [56-61].

RNA-Binding Proteins (RBPs)

Proteins like LIN28 bind to pre-miRNAs, inhibiting Drosha/Dicer processing and promoting miRNA degradation. Conversely, hnRNP A1 and KSRP stabilize pre-miRNAs, enhancing maturation. In plants, DRB1 (HYL1) ensures accurate DCL1 cleavage, while DRB2 fine-tunes miRNA abundance. RBPs also guide miRNAs to specific subcellular locations, influencing their incorporation into RISCs [62-66].

Small RNA Stability Modifications

3′-end methylation by HEN1 protects miRNAs from exonucleolytic decay, a critical step in maintaining miRNA longevity. Conversely, terminal uridylation (mediated by TUTases) or adenylation marks miRNAs for degradation, providing a rapid turnover mechanism. Environmental stresses can shift this balance;

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for example, hypoxia increases uridylation of specific miRNAs, reducing their stability and altering gene expression profiles [67-69].

Functions in Plant Growth and Development

Leaf Development

miRNAs play a crucial role in regulating leaf development by controlling key transcription factors. For example, miR166 and miR165 target HD-ZIP III family genes, which are essential for establishing leaf polarity—determining the adaxial (upper) and abaxial (lower) sides of leaves (Figure 2). Overexpression or suppression of these miRNAs leads to abnormal leaf shapes, such as curled or radialized leaves [70-72] Additionally, miRNAs like miR319 regulate TCP TFs, influencing cell proliferation and leaf size. The precise spatial and temporal expression of these miRNAs ensures proper leaf morphogenesis during plant growth. Environmental factors such as light and stress can modulate miRNA levels, further fine-tuning leaf development [73-75]. The regulation of leaf development by miR166/165 is crucial because HD-ZIP III transcription factors control not just polarity but also vascular tissue formation. Without proper miRNA-mediated control, leaves may develop improperly, reducing photosynthesis efficiency. Additionally, these miRNAs help plants adapt to environmental stresses by modulating leaf structure under varying light conditions. Their role ensures balanced growth between different leaf layers, optimizing light capture and gas exchange[70-75].

Root Architecture

miRNAs are central to root development, particularly in lateral root formation. The miR390-TAS3-ARF pathway is a key regulatory module where miR390 triggers the production of trans-acting small interfering RNAs (tasiRNAs) from the TAS3 gene. These tasiRNAs then suppress AUXIN RESPONSE FACTORs (ARFs), particularly ARF2, ARF3, and ARF4, which are negative regulators of lateral root growth (Figure 2). By modulating auxin signaling, this pathway ensures proper root branching and soil exploration. Mutations in this pathway result in altered root systems, affecting nutrient uptake and plant stability. The miR390-TAS3-ARF pathway is vital because auxin distribution dictates where lateral roots emerge, improving nutrient and water absorption. Without this regulation, roots may grow unevenly, weakening plant stability [72,76-79].

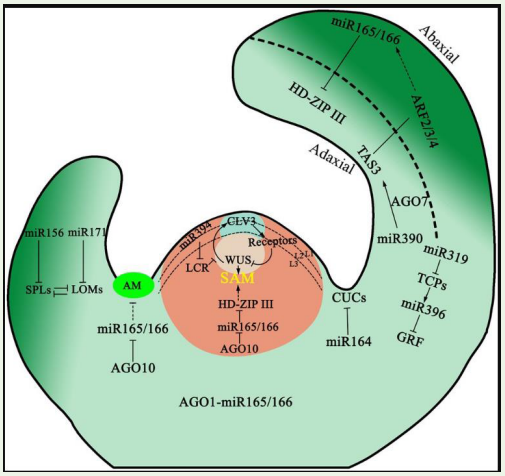

Figure 2: Regulatory network of small RNAs in shoot apical meristem and leaf development. The diagram illustrates key small RNA-mediated pathways controlling SAM maintenance, leaf polarity establishment, and trichome initiation. miR394 represses LCR to activate WUS/CLV3 signaling, while AGO10 sequesters miR165/166 to regulate meristem activity. HD-ZIP III and ARF2/3/4 define adaxial-abaxial leaf domains under the control of miR165/166 and TAS3 ta-siRNA, respectively. miR164, miR319/miR396, and miR156/miR171 further modulate meristem initiation, leaf growth, and trichome formation. Solid arrows indicate positive regulation; dashed lines with perpendicular ends denote inhibitory interactions. Figure is adapted from Dong et al. 2022 [72].

Juvenile-to-Adult Transition

The transition from juvenile to adult vegetative phases is tightly controlled by miR156, which targets SQUAMOSA PROMOTER BINDING PROTEIN-LIKE (SPL) transcription factors. High levels of miR156 in young plants suppress SPLs, maintaining juvenile traits like leaf shape and delayed flowering. As the plant ages, miR156 levels decline, releasing SPL repression and allowing the expression of adult-phase genes. Some SPLs also promote flowering, linking vegetative phase change with reproductive timing. Environmental cues such as light and temperature can influence miR156 accumulation, affecting developmental timing. The gradual decline of miR156 ensures that plants transition to maturity at the right time, preventing premature flowering under unfavourable conditions. This regulation is important because juvenile and adult leaves often have different shapes and functions, affecting overall plant fitness. Environmental factors like temperature can influence miR156 levels, allowing plants to adjust their growth phases in response to seasonal changes [80-82].

Floral Induction

miR172 plays a pivotal role in promoting flowering by repressing APETALA2 (AP2)-like transcription factors, which act as floral repressors. As plants mature, miR172 levels increase, reducing AP2-like activity and allowing floral meristem identity genes (e.g., LFY, AP1) to be expressed. This regulatory switch ensures that flowering occurs at the appropriate developmental stage. Some AP2-like genes also regulate floral organ identity, making miR172 crucial for both floral timing and patterning. By suppressing AP2-like genes, miR172 ensures flowering occurs only when the plant has sufficient energy and resources. This prevents wasted reproductive efforts in poor growing conditions. Additionally, since AP2-like genes also affect flower structure, miR172 indirectly ensures proper floral organ development. Its role is critical for synchronizing flowering with pollinators and optimal seed-setting conditions [83-86].

Floral Organ Identity

miRNAs contribute to floral patterning by regulating key developmental genes. miR172, for instance, fine-tunes AP2 expression, ensuring proper sepal and petal formation. Another example is miR159, which targets MYB transcription factors to control stamen development. Disruption of these miRNAs leads to floral abnormalities, such as homeotic transformations (e.g., petals turning into stamens). The precise spatiotemporal expression of these miRNAs ensures correct floral organ specification. Proper floral organ formation, controlled by miR172 and miR159, is essential for successful pollination and seed production. If floral organs develop

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incorrectly, pollination efficiency drops, reducing yield in crop plants. These miRNAs also help maintain species-specific flower shapes, which are often key for attracting the right pollinators [85-88].

Seed Development

During embryogenesis, miRNAs such as miR160 and miR167 regulate ARF genes to modulate auxin signaling, which is critical for proper seed formation. miR160 targets ARF10/16/17, affecting embryo patterning, while miR167 controls ARF6/8, influencing endosperm development. Imbalances in these miRNAs can lead to seed abortion or abnormal embryo morphology. Auxin-miRNA crosstalk ensures coordinated seed growth and nutrient allocation.The role of miR160 and miR167 in seed development is critical because auxin signaling determines embryo orientation and nutrient flow. Disruptions can lead to malformed seeds or even complete seed abortion, affecting plant propagation. Since seeds are crucial for the next generation, these miRNAs help maintain high germination rates and seedling vigor, ensuring species survival [89-93]. (Table 1) clearly indicates various functions of miRNAs in plant growth and developmental processes.

In the shoot apical meristem (SAM), miR394 is synthesized in the protoderm and moves to subtending cells, where it represses LEAF CURLING RESPONSIVENESS (LCR). This repression activates WUSCHEL (WUS), maintaining stem cell identity and promoting CLAVATA3 (CLV3) peptide expression. AGO10 specifically sequesters miR165/166 in meristematic cells, counteracting its activity to regulate SAM and axillary meristem (AM) development. In contrast, AGO1 is broadly expressed in the apex and recruits miR165/166 to form the RISC, ensuring proper meristem function (Figure 2). During leaf primordia formation, HD-ZIP III transcription factors are restricted to the adaxial (upper) side by miR165/166, while ARF2/3/4 are confined to the abaxial (lower) side via TAS3-derived trans-acting small interfering RNAs (ta-siRNAs). Additionally, miR164 post-transcriptionally regulates two NAC-domain transcription factors, influencing embryonic meristem initiation, boundary size control, and cotyledon establishment. Leaf development is further modulated by miR319 and miR396, which target TCP and GRF genes, respectively, coordinating cell proliferation and differentiation. Meanwhile, miR156 and miR171 synergistically regulate trichome initiation by suppressing SPL and LOM [70-93].

miRNAs in Stress Responses

Drought & Salinity (miR169-NF-YA Pathway)

miR169 plays a critical role in drought and salinity tolerance by downregulating NF-YA transcription factors, which are involved in stress-responsive gene expression. Under water-deficient conditions, plants increase miR169 levels to suppress NF-YA, conserving energy by reducing non-essential metabolic processes. This regulation helps maintain cellular stability by preventing excessive stress-induced damage. Additionally, miR169-mediated control ensures that only essential stress-response genes are activated, improving survival rates in harsh environments. Some crop plants genetically engineered to overexpress miR169 show enhanced drought resistance, highlighting its agronomic importance. The evolutionary conservation of miR169 across plant species suggests its fundamental role in abiotic stress adaptation. Field studies indicate that natural variants with higher miR169 expression perform better in arid regions, offering potential for crop improvement programs[94-97].

Nutrient Deficiency (miR399-PHO2 Regulation)

Under phosphate starvation, plants upregulate miR399, which suppresses PHO2, a negative regulator of phosphate transporters. By inhibiting PHO2, miR399 allows increased phosphate uptake from the soil, ensuring proper growth even in low-nutrient conditions. This miRNA-mediated regulation is crucial because phosphorus is essential for ATP synthesis and nucleic acid formation. Interestingly,

Table 1: Key miRNAs and Their Functions in Plant Growth and Development

Developmental Process	Key miRNA(s)	Target Gene(s)	Function	Consequence of Dysregulation	Environmental Influence
Leaf Development	miR165/ miR166	HD-ZIP III family	Regulates leaf polarity (adaxial-abaxial) and vascular tissue formation	Abnormal leaf shapes (curled, radialized leaves)	Light and stress modulate miRNA levels
	miR319	TCP transcription factors	Controls cell proliferation and leaf size	Altered leaf morphology	–
Root Architecture	miR390	TAS3 → ARF2/3/4 (via tasiRNAs)	Promotes lateral root formation via auxin signaling	Reduced root branching, impaired nutrient uptake	Soil conditions (e.g., low phosphorus) affect regulation
Juvenile-to-Adult Transition	miR156	SPL transcription factors	Maintains juvenile phase; decline triggers adult traits	Delayed or premature flowering, altered leaf morphology	Light and temperature influence miR156 levels
Floral Induction	miR172	AP2-like transcription factors	Represses floral inhibitors, promotes flowering	Delayed flowering, improper floral timing	Ensures flowering under optimal energy conditions
Floral Organ Identity	miR172	AP2	Regulates sepal/petal formation	Homeotic transformations (e.g., petals → stamens)	–
	miR159	MYB transcription factors	Controls stamen development	Abnormal stamens, reduced fertility	–
Seed Development	miR160	ARF10/16/17	Regulates embryo patterning	Seed abortion, abnormal embryo morphology	–
	miR167	ARF6/8	Influences endosperm development	Impaired nutrient allocation, defective seeds	–

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miR399 is also transported from shoots to roots through the phloem, coordinating systemic phosphate distribution. This mechanism demonstrates how miRNAs help plants optimize nutrient use efficiency under stress.Recent research shows that miR399 expression patterns can serve as early indicators of phosphorus deficiency, potentially enabling precision agriculture approaches. The discovery of natural allelic variations in miR399 genes among crop wild relatives may provide new genetic resources for breeding nutrient-efficient varieties[98-101].

Pathogen Defense (miR393-Auxin Signaling)

When pathogens attack, plants elevate miR393 to suppress auxin receptor genes (e.g., TIR1/AFB), reducing auxin signaling. Since many pathogens exploit auxin pathways to weaken plant immunity, miR393 acts as a defense mechanism by disrupting this manipulation. The downregulation of auxin signaling also triggers the activation of PR (Pathogenesis-Related) genes, enhancing resistance. Studies show that plants with higher miR393 levels exhibit stronger antibacterial and antifungal responses. This miRNA thus serves as a molecular switch that prioritizes defense over growth during infections.The speed of miR393 induction varies among plant species, with faster responders showing greater disease resistance. Agricultural applications could include developing miR393-based biomarkers for early disease detection or engineering crops with tunable miR393 expression for enhanced field resistance. In *Gossypium hirsutum*, ghr-miR393-GhTIR1 module regulates plant defense against *Verticillium dahliae*by modulating auxin signaling. Overexpression of ghr-miR393 or knockdown of GhTIR1 activates ICS1 and NPR1, key components of SA-mediated defense. This suppression of auxin signaling (via GhTIR1) enhances resistance by derepressing SA-dependent pathways (Figure 3)[102-104].(Table 2) clearly indicates various roles of miRNAs in biotic and abiotic stress responses.

Evolutionary Conservation and Biotechnological Applications

Evolutionary Conservation of miRNAs

The conservation of miRNAs like miR156 and miR172 across land plants highlights their fundamental roles in regulating essential biological processes. These miRNAs have been preserved over millions of years of evolution, suggesting strong selective pressure to maintain their functions in growth, development, and stress responses. Their conserved sequences and target genes across diverse species indicate a shared regulatory mechanism that has been fine-tuned through evolutionary time. Studying these miRNAs provides insights into the core genetic pathways that govern plant physiology. Additionally,

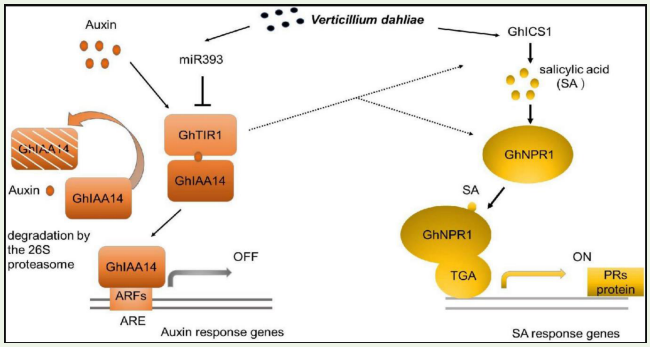

Figure 3: Model of ghr-miR393-GhTIR1 in plant immunity against *Verticillium dahliae*. ghr-miR393 targets GhTIR1, suppressing auxin signaling and activating ICS1-NPR1-mediated SA defense. Dashed lines indicate enhanced ICS1/NPR1 expression upon ghr-miR393 overexpression or GhTIR1 knockdown. ARE (auxin response element) may contribute to pathway regulation. Figure is adapted from Shi et al. 2022 [104].

their conservation allows researchers to leverage knowledge from model organisms to understand their roles in economically important crops. The stability of these regulatory molecules across species also suggests that manipulating them could have predictable and widespread effects in plant biotechnology[105-107].

Biotechnological Applications of Engineered miRNAs

Engineered miRNAs offer a powerful tool for precise genetic modification in crops, enabling targeted enhancement of stress tolerance and yield. By designing artificial miRNAs, scientists can silence or modulate specific genes involved in stress responses, nutrient utilization, or developmental pathways without introducing foreign proteins. This approach reduces unintended effects compared to traditional transgenic methods. Engineered miRNAs can be tailored to fine-tune gene expression, optimizing traits such as drought resistance, disease immunity, or flowering time. Their small size and high specificity make them easier to incorporate into plant genomes while minimizing regulatory concerns. Furthermore, since endogenous miRNA pathways are already present in plants, engineered miRNAs integrate seamlessly into existing regulatory networks. This technology holds great promise for sustainable agriculture by improving crop resilience and productivity under challenging environmental conditions [108-110].

Future Perspectives

Expanding miRNA Discovery Through Single-Cell Sequencing

Future research should leverage single-cell RNA sequencing to uncover cell-type-specific miRNA expression patterns, providing

Table 2: miRNAs and their role in biotic and abiotic stresses

Stress Type	Key miRNA(s)	Target Gene(s)/Pathway	Mechanism of Action	Physiological Outcome	Agricultural Significance
Drought & Salinity	miR169	NF-YA transcription factors	Downregulates NF-YA to conserve energy under stress	Enhances cellular stability, reduces metabolic stress	Overexpression improves drought tolerance; conserved across species
Phosphate Deficiency	miR399	PHO2 (ubiquitin E2 conjugase)	Suppresses PHO2, upregulating phosphate transporters	Increases phosphate uptake and root-to-shoot allocation	Potential for breeding nutrient-efficient crops; phloem-mobile
Pathogen Defense	miR393	TIR1/AFB (auxin receptors)	Reduces auxin signaling to block pathogen manipulation	Activates PR genes, strengthens immunity	Engineered crops show enhanced disease resistance

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unprecedented resolution in understanding developmental and stress responses. This approach will reveal how miRNAs fine-tune gene regulation in individual cell types, such as root hairs or guard cells, under varying conditions. Integrating spatial transcriptomics could further map miRNA activity across tissues, enhancing our knowledge of their localized functions. Such advancements will enable the design of precision-engineered miRNAs for targeted crop improvement.

Deciphering miRNA Crosstalk with Epigenetic Mechanisms

Exploring the interplay between miRNAs and epigenetic modifications (DNA methylation, histone marks) will uncover new regulatory layers in stress adaptation. Future studies should investigate how environmental cues alter miRNA expression via chromatin remodeling and how these changes are inherited. Understanding this crosstalk could lead to epigenetic editing strategies that enhance stress memory in crops. Additionally, identifying miRNAs that regulate epigenetic modifiers may reveal novel targets for biotechnology applications.

Developing miRNA-Based Biomarkers for Precision Agriculture

miRNA expression profiles could serve as early diagnostic biomarkers for stress conditions, nutrient deficiencies, or disease susceptibility. Future work should focus on field-deployable detection methods, such as portable PCR or nanosensors, to monitor miRNA dynamics in real time. This could enable preemptive agricultural interventions, optimize resource use and minimize yield losses. Machine learning models trained on miRNA expression data may further improve predictive accuracy for crop management.

Engineering Synthetic miRNA Networks for Climate Resilience

Advancements in synthetic biology could allow the design of artificial miRNA circuits that dynamically respond to environmental triggers (e.g., drought, heat). Future efforts should focus on creating feedback-regulated miRNA systems that fine-tune stress responses without compromising growth. Combining multiple engineered miRNAs into synergistic networks may enhance multi-stress tolerance. Field trials of such designs will be critical to assess their efficacy under real-world conditions.

Harnessing miRNA-Mediated RNAi for Pest and Pathogen Control

Future applications could exploit miRNA pathways to develop RNAi-based biopesticides that target herbivores or pathogens while sparing beneficial organisms. Research should optimize delivery methods, such as nanoparticle carriers or root uptake, to ensure stability and specificity. Engineered miRNAs could also silence virulence genes in pathogens, offering a sustainable alternative to chemical pesticides. Regulatory frameworks must evolve to address the ecological implications of such technologies.

Exploring Horizontal miRNA Transfer in Plant-Microbe Interactions

Emerging evidence suggests miRNAs may be exchanged between plants and associated microbes, influencing symbiosis or defense. Future studies should investigate the mechanisms and functional consequences of this cross-kingdom communication. Understanding how microbial miRNAs modulate host gene expression could lead to novel biofertilizers or biocontrol agents. This field may uncover new dimensions of plant-microbe coevolution.

Integrating miRNA Editing with CRISPR-Cas Technologies

Combining CRISPR-based genome editing with miRNA manipulation could enable simultaneous tuning of multiple gene networks. Future research should develop tools for precise miRNA gene editing (e.g., promoter modifications, stem-loop alterations) to optimize expression levels. Dual-function systems, where CRISPR guides and miRNAs target complementary pathways, may enhance trait stacking in crops. Ethical and regulatory considerations will be paramount in deploying such advanced technologies.

Bridging miRNA Research with Crop Wild Relatives for Breeding

Future breeding programs should mine miRNA diversity in crop wild relatives to identify natural alleles associated with stress resilience. Comparative genomics and pan-miRNAome analyses could reveal conserved and species-specific regulatory nodes. Introgression of beneficial miRNA variants via marker-assisted selection may accelerate the development of climate-smart crops. This approach aligns with sustainable agriculture by reducing reliance on transgenic modifications.

Conclusion

MicroRNAs (miRNAs) play vital roles in plant biology, regulating gene expression through mRNA cleavage or translational repression to control growth, development, and stress responses. Their evolutionary conservation highlights their importance across species, while biotechnological advances demonstrate their potential for engineering stress-resistant crops. This review explores miRNA-mediated regulation, emphasizing their role in plant physiology and agricultural innovation. Emerging technologies, such as single-cell sequencing and synthetic miRNA networks, may further enhance crop resilience and productivity. Understanding miRNAs is key to addressing global food security through precision breeding and biotechnology.

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