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From Regulatory Networks to Precision Breeding: Integrating miRNA and Gene Editing for Trait Improvement in Forest Trees

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Abstract. In recent years, with the development of high-throughput sequencing and molecular biology techniques, researchers have identified a large number of miRNA sequences in plants, which play crucial roles in developmental regulation, signal transduction, stress response, and maintenance of nutrient homeostasis. Compared with crops, research on miRNA function in forest trees started later due to their long life cycle and complex genome. However, they have unique regulatory patterns in adaptive evolution, morphological differentiation and stress resistance formation. This article systematically summarizes the functions of plant miRNAs in developmental and hormonal signaling pathways, and in abiotic and biotic stresses, focusing on their mechanisms of action within the forest tree gene regulatory network. Meanwhile, combining the latest advancements in gene editing and viral vector technologies, this study analyzes the application prospects of miRNA-mediated gene silencing in molecular design breeding, and proposes a strategic framework for the precise improvement of complex traits in forest trees by integrating miRNA regulatory modules with CRISPR/Cas technology, providing new theoretical and technical support for molecular breeding of forest trees.

Keywords: Gene editing; miRNA; target gene regulation; abiotic stress regulation.

1. Introduction

Plant miRNAs, as highly conserved and highly specific endogenous small RNA molecules, are important regulatory hubs for the formation of complex traits. In plant life activities, they couple transcriptional, post-transcriptional, and epigenetic regulation to construct multi-level gene networks [1-2]. miRNAs influence many gene families, such as the SPL, ARF, NAC, and HD-ZIP families, through negative regulatory modes, thereby regulating developmental processes, organ structure, and stress responses [3-4].

In forest trees, the long developmental cycle, high genotypic heterogeneity, and complex alternative splicing make miRNAs important regulatory nodes connecting gene function and complex traits. For example, in woody plants such as poplar, eucalyptus, and fir, miR156, miR172, and miR397 have all been found to be closely related to apical dominance, secondary growth, and lignification processes [5-6]. Thus, miRNA research provides a new tool for elucidating the mechanisms of long-term trait formation and adaptive evolution [7-8].

With the advancement of molecular design breeding, the use of miRNA network regulation to achieve the design of target traits (such as early flowering, stress resistance, and lignin accumulation balance) has become a new direction in forest tree breeding [9-10]. At the same time, the combination of viral vector-induced gene silencing (VIGS) and CRISPR/Cas gene editing technology has made the analysis of miRNA generation, processing and target regulation more efficient, laying the foundation for the "programmable design" of complex forest tree genomes.

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2. The role of miRNA in plant development regulation

2.1. miR156–SPL module and developmental stage transition

miR156 is considered one of the key factors in the transition from vegetative to reproductive growth in plants. It regulates bud differentiation, internode elongation, and flowering time by targeting members of the SPL (SQUAMOSA Promoter Binding Protein-Like) gene family. In Arabidopsis thaliana, miR156 directly silences more than ten SPL genes [11-12], restricting early bud growth and inhibiting floral organ differentiation, thereby delaying flowering. In poplar and willow, this module further controls tillering, apical dominance reduction, and branch angle formation, which are closely related to the degree of lignification [13-14].

miR156 and miR172 constitute a two-layer regulatory system for plant development. As plants age, the expression of miR156 gradually decreases, while the expression of SPL increases, thereby activating miR172. The latter initiates flowering by inhibiting AP2-type transcription factors. This "miR156–SPL–miR172–AP2" cascade regulatory network is conserved in many woody plants, providing potential molecular targets for regulating the developmental cycle, flowering period, and flowering synchronicity of forest trees [15-16].

2.2. miR159 and miR164: Regulation of reproductive structure and maturation

miR159 targets GAMYB transcription factors, preventing their overexpression in vegetative tissues that leads to growth inhibition, and its balanced regulation ensures normal pollen development [17-18]. In gramineous crops such as rice and barley, this mechanism stabilizes the anther differentiation process; in woody plants, such as Sapindaceae and Fagaceae species, the GAMYB gene is also regulated by miR159 during flower bud induction, which is of great value for molecular optimization of early flowering traits [19-20].

miR164 targets the NAC gene and regulates fruit ripening and organ differentiation by upregulating the ethylene pathway [21-22]. In particular, in fruit trees and woody economic forests (such as peach, apple, and olive), the miR164–NAC module and the miR319–TCP module work together to coordinate leaf senescence and floral organ stability, providing a molecular pathway for regulating the reproductive cycle of trees and fruit quality [23-24].

2.3. Tissue Differentiation and Vascular Construction of miR165/166

miR165/166 are widely found in terrestrial plants and affect leaf dorsal and ventral polarity, vascular bundle formation, and lignification by targeting HD-ZIP class III transcription factors (such as REV, PHB, and PHV) [25-26]. These miRNAs play a key role in the secondary growth of woody plants. By editing miR165/166 sites using CRISPR/Cas, it is possible to achieve fine regulation of vessel arrangement, wood density, and mechanical strength, laying the foundation for the improvement of structural timber and fiber forest varieties [27-28].

3. Functional regulation of miRNAs in plant hormone signal transduction

Plant growth and development are regulated by the interaction of multiple hormone signals (such as auxin, gibberellin, cytokinin, abscisic acid, ethylene and brassinolide) [29-30]. miRNAs form a multi-layered feedback regulatory system by targeting key factors in hormone signaling pathways.

3.1. miRNA network of the auxin pathway

The miR160 targets ARF10/16/17, while miR167 targets ARF6/8, jointly regulating adventitious root formation and floral organ morphology. In forest trees, this mechanism extends to root system construction and nutrient uptake regulation [31-32]. Overexpression of miR160 enhances lateral root density and improves drought resistance, while inhibition of miR167 accelerates apical growth, demonstrating its important role in root-crown allocation.

The miR390-mediated tasiRNA–ARF pathway further refines the auxin response system [33-34]. miR390 depends on the cleavage of the non-coding RNA tasi3 to regulate the expression of downstream ARF gene clusters, thereby finely controlling lateral root development. This network has been shown to be conserved in poplar and Chinese fir and is an important molecular control mechanism for root development optimization [35-36].

3.2. Interactive Regulation of Other Hormonal Signaling

miR159 interacts with gibberellin signaling to regulate seed germination and flowering. Gibberellin treatment upregulates miR159, promoting GAMYB silencing and thus preventing premature flowering or premature reproduction in plants [37-38].

In addition, miR172 is co-regulated by cytokinins and ethylene, and can promote seed maturation and yield by regulating AP2 transcription factors. miR394, miR319, etc., are involved in the jasmonic acid pathway to regulate resistance. The complex network constructed by the interaction of hormone signals and miRNAs makes them a regulated "signal valve" in molecular breeding [39-40].

4. The role of plant miRNAs in abiotic stress responses

When plants are fixed in the environment and face abiotic stresses such as drought, salinity, extreme temperatures, and nutrient deficiencies, miRNAs adaptively regulate related genes to reshape physiological metabolism through expression.

4.1. Drought stress

Drought is a major factor limiting plant yield and forest growth. Studies have shown that upregulation of miR160, miR167, and miR393 can promote root development and growth hormone accumulation, while downregulation of miR169 leads to -a reduction in the NF YA5 transcription factor, thereby regulating water use efficiency. Arabidopsis thaliana overexpressing miR169 is drought sensitive, while -overexpression of NF YA5 enhances drought tolerance. Similar phenomena have been found in rice, poplar, and other plants, suggesting that the miR169 family may be a "core module" in the evolution of stress response [41-42].

miR535, miR408, and miR394 have all exhibited drought-inducing properties in various plants. By regulating these miRNAs, the survival ability of trees under drought or saline conditions can be specifically enhanced. For example, overexpression of miR408 in eucalyptus can improve water use efficiency and enhance the activity of protective enzymes [43-44].

4.2. Temperature Stress

Both low-temperature and high-temperature stress can induce specific miRNA regulatory networks. miR398 responds to heat stress by inhibiting CSD1/CSD2 to activate the heat shock protein (HSP) system, thereby enhancing heat tolerance. In cotton and poplar, miR160 maintains stable anther development under heat stress by regulating the ARF pathway [45-46]. Under cold stress, miR168/171 exhibit opposite regulatory patterns in different species: upregulation in poplar promotes frost resistance, while downregulation in rice accelerates ripening and increases yield. This indicates that miRNA regulation has significant species specificity. In addition, some specific miRNAs, such as miR69.5p, exhibit dynamic responses at different time stages, indicating that miRNAs not only regulate homeostasis during temperature adaptation but also participate in time-dependent signal transduction processes.

4.3. Nutritional Deficiency and Ion Homeostasis

miR399 is a typical miRNA that senses phosphorus deficiency; its upregulation inhibits PHO2 gene expression and enhances phosphorus uptake. miR395 is upregulated under sulfur deficiency or oxidative stress, regulating sulfate transporter genes and maintaining sulfur homeostasis [47-48].

In legumes, miR2119 and miR5213 participate in the regulation of aluminum toxicity stress, improving tolerance to acidic soil environments by acting on F-box proteins. In addition, under sufficient nitrogen fertilizer conditions, miR528 strengthens stem mechanical strength by targeting the lignin synthesis gene ZmLAC3, which helps improve lodging resistance [49-50].

5. Functions of miRNAs in biological stress response and disease resistance

When plants are infected by pathogens, they rapidly activate a defense system centered on miRNAs. miRNAs induce the expression of defensive genes by recognizing pathogen-associated molecular patterns (PAMPs), thereby initiating systemic resistance.

The miR393 is significantly upregulated in Arabidopsis thaliana when infected by pathogens, targeting the auxin receptor TIR1 to inhibit auxin signaling, thereby indirectly enhancing the defense response. miR160, miR167, and miR159 are also upregulated in pathogen sensing and participate in regulating disease-related hormone pathways (such as SA/JA). On the other hand, viral infection can evade immunity by inhibiting host miRNA processing (such as DCL1 and AGO1), and host plants have also evolved specific miRNAs such as miR444, which interfere with viral replication by targeting the MADS transcription factor and affecting the RDR1 gene.

In forest trees, such as poplar and citrus, the miR482 and miR2118 families can target the disease-resistant NBS-LRR gene cluster to balance defense and growth. By regulating the levels of these miRNAs through gene editing, disease and pest resistance can be improved without affecting growth, which has important application prospects.

6. The integration of miRNA and gene editing technology: a new direction in molecular design breeding.

The integration of miRNA and gene editing technologies has opened up new directions for molecular design breeding of forest trees. Virus-induced gene silencing (VIGS) systems provide a highly efficient platform for studying miRNA function in most forest trees that are difficult to genetically transform. By modifying engineered vectors such as tobacco stripe mosaic virus (TRV), potato virus X (PVX), or barley stripe mosaic virus (BSMV), heterologous expression of specific miRNA fragments or their precursor structures can be achieved, triggering reversible silencing of target genes[51-52]. This allows for rapid validation of miRNA function without relying on stable genetic transformation. For example, VIGS has been used to elucidate the regulatory role of miR166 in vascular differentiation in poplar, and to regulate the expression of drought-resistance-related miRNAs in black locust and Chinese fir. Combining VIGS with bioinformatics target prediction enables high-throughput screening and precise validation of miRNA regulatory networks, providing an efficient tool for studying the gene function of complex traits in forest trees [53-54].

With the maturation of the CRISPR/Cas system, miRNA research has entered a "programmable" stage. By editing miRNA genes or their target regions, their regulatory mechanisms can be directly elucidated. For example, -modifying the miR169 site targeting the NF YA5 gene can block miRNA-mRNA pairing and restore stress resistance. Simultaneously, artificial miRNAs (amiRNAs) can mimic natural hairpin structures to directionally silence target genes, exhibiting higher specificity and biosafety. Furthermore, systems such as CRISPRa/Cas13d enable precise regulation of miRNA transcription. In poplar gene editing research, knocking out the miR156 regulatory domain led to sustained high expression of the SPL gene, significantly shortening the juvenile stage and promoting early flowering and rapid lignin accumulation, demonstrating the enormous potential of miRNA networks in the remodeling of complex traits in forest trees .

7. Conclusion

The deepening of miRNA research has propelled plant molecular breeding to a new stage. It not only reveals the molecular basis of forest tree growth, development, and stress adaptation, but also provides programmable regulatory elements for molecular design breeding. By combining miRNA target regulation with CRISPR/Cas technology and the VIGS system, complex traits such as lignification, stress resistance, early flowering, and nutrient utilization can be precisely controlled at the gene level. Future molecular design breeding should use the "miRNA-target gene-phenotype" framework as its core, combining small RNA sequencing, systems biology modeling, VIGS dynamic validation, and precise CRISPR intervention to achieve a closed loop from gene regulatory network analysis to targeted trait improvement. By constructing a forest tree-specific miRNA regulatory module library and intelligent prediction system, miRNAs can be elevated from natural regulatory factors to programmable breeding design elements, driving forest tree genetic improvement from empirical selection to model-driven precision design.

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