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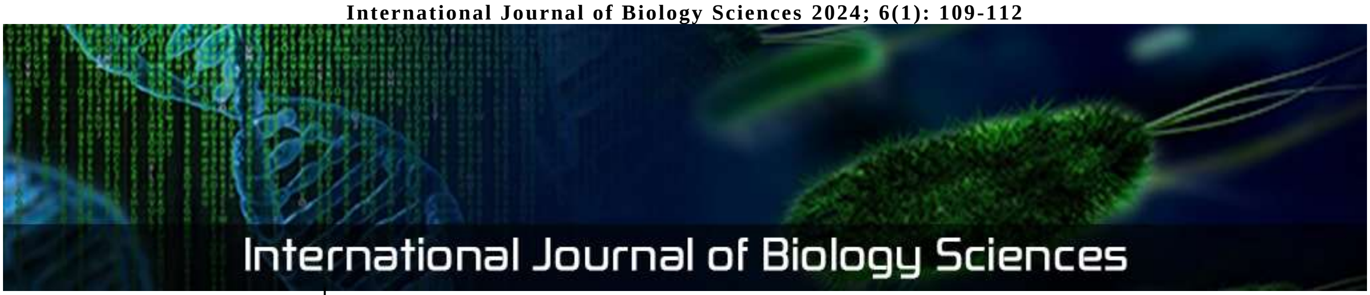

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The role of small RNAS in regulating disease resistance in plants

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Abstract

Small RNAs (sRNAs) have emerged as crucial regulators of gene expression in plants, playing significant roles in various biological processes, including disease resistance. This paper provides a comprehensive overview of the mechanisms by which sRNAs, including microRNAs (miRNAs) and small interfering RNAs (siRNAs), regulate plant immune responses. We discuss the biogenesis and functional roles of these sRNAs, highlighting recent advancements in understanding their contributions to plant-pathogen interactions. Furthermore, we explore the potential of sRNA-based strategies for enhancing disease resistance in crops, addressing the challenges and future directions in this rapidly evolving field.

Keywords: Small RNAs, microRNAs, small interfering RNAs, disease resistance, plant immunity, biogenesis, gene regulation, plant-pathogen interactions

Introduction

Plant diseases caused by various pathogens, including bacteria, fungi, viruses, and nematodes, present significant challenges to global agriculture, leading to substantial yield losses and threatening food security. Traditional methods for developing disease-resistant crop varieties, such as selective breeding and the use of chemical pesticides, often fall short due to time constraints, pathogen adaptation, and environmental concerns. Consequently, there is an urgent need for innovative approaches to enhance disease resistance in plants. Small RNAs (sRNAs) have emerged as pivotal regulators of gene expression, influencing a multitude of biological processes, including development, stress responses, and immune regulation. These short, non-coding RNA molecules, typically 20-24 nucleotides in length, can be broadly categorized into two main classes: microRNAs (miRNAs) and small interfering RNAs (siRNAs). Both types of sRNAs function through RNA-induced silencing complexes (RISCs), guiding these complexes to complementary messenger RNAs (mRNAs) to trigger mRNA degradation or translational repression. The discovery and characterization of miRNAs and siRNAs have revolutionized our understanding of post-transcriptional gene regulation in plants. MiRNAs are derived from single-stranded RNA precursors that form hairpin structures, which are processed by Dicer-like enzymes to produce mature miRNA duplexes. These mature miRNAs play crucial roles in modulating the expression of genes involved in plant immunity, development, and hormonal signaling pathways. SiRNAs, on the other hand, originate from double-stranded RNA (dsRNA) precursors and are similarly processed by Dicer-like enzymes. SiRNAs are primarily involved in antiviral defense, transposon silencing, and the regulation of endogenous genes. Research over the past decade has significantly advanced our understanding of the roles of sRNAs in plant immunity. Studies have demonstrated that sRNAs can fine-tune the expression of resistance (R) genes, which encode proteins responsible for recognizing pathogen-derived molecules and initiating defense responses. For example, in tomato, miR482 and miR2118 regulate the levels of nucleotide-binding leucine-rich repeat (NLR) R genes, thereby modulating the plant's resistance to pathogens such as *Phytophthora infestans*. Similarly, siRNAs have been shown to participate in the amplification of immune signals through the production of phased secondary siRNAs (phasiRNAs), which target additional defense-related mRNAs. The intricate regulatory networks mediated by sRNAs highlight the dynamic nature of plant immune responses. MiRNAs have been found to interact with hormonal signalling pathways, including those involving salicylic acid (SA), jasmonic acid (JA), and ethylene (ET), which are critical for coordinating defense mechanisms. The regulation of these pathways by miRNAs allows plants to prioritize immune responses over growth and other physiological processes during pathogen attack. Moreover, recent discoveries have revealed that sRNAs can contribute to transgenerational immune priming, where plants exposed to pathogens pass on enhanced resistance traits to their offspring through epigenetic modifications. This form of memory ensures that subsequent generations are better equipped to handle similar pathogenic challenges. The practical applications of sRNA research in agriculture are vast. Genetic engineering techniques, such as CRISPR-Cas9, have been employed to manipulate sRNA pathways, enhancing disease resistance in crops. For instance, knocking out miRNA genes that suppress R genes can lead to increased expression of these R genes and improved resistance to pathogens. Additionally, the exogenous application of synthetic sRNAs targeting pathogen genes has shown potential as a novel strategy for protecting crops from viral infections.

Main objective

The main objective of this paper is to explore and elucidate the mechanisms by which small RNAs (sRNAs) regulate disease resistance in plants, highlighting their biogenesis, functional roles, and potential applications in enhancing crop resilience through genetic and biotechnological approaches.

Biogenesis and types of small RNAs

Small RNAs (sRNAs) are crucial regulators of gene expression in plants, playing significant roles in various biological processes, including development, stress responses, and disease resistance. They are short, non-coding RNA molecules, typically 20-24 nucleotides in length, and can be broadly categorized into microRNAs (miRNAs) and small interfering RNAs (siRNAs). Understanding their biogenesis and functional roles is essential for appreciating how plants regulate gene expression at the post-transcriptional level. The biogenesis of miRNAs begins with the transcription of miRNA genes by RNA polymerase II, producing primary miRNAs (pri-miRNAs) that form characteristic hairpin structures. These pri-miRNAs are processed in the nucleus by a protein complex involving Dicer-like 1 (DCL1), Hyponastic Leaves 1 (HYL1), and Serrate (SE). This processing results in precursor miRNAs (pre-miRNAs), which are further cleaved by DCL1 to generate mature miRNA duplexes. One strand of the duplex, known as the guide strand, is incorporated into the RNA-induced silencing complex (RISC), while the other strand is typically degraded. The mature miRNA within the RISC then guides the complex to complementary target mRNAs, leading to their degradation or translational repression. In contrast, siRNAs are derived from long double-stranded RNA (dsRNA) molecules, which can originate from various sources, including viral replication intermediates, transposons, and endogenous loci. The dsRNA precursors are processed by Dicer-like (DCL) enzymes into siRNA duplexes. Similar to miRNAs, one strand of the siRNA duplex is incorporated into the RISC, directing it to target mRNAs for cleavage. SiRNAs are involved in a range of processes, including antiviral defense, transposon silencing, and regulation of gene expression. Comparing these mechanisms with previous studies highlights significant advancements in our understanding of sRNA biogenesis. Earlier research primarily focused on the discovery and characterization of miRNAs and siRNAs, elucidating their basic functions and regulatory roles. For instance, early studies in Arabidopsis thaliana revealed the involvement of DCL1 in miRNA processing and identified numerous miRNAs that regulate key developmental processes. Similarly, the role of siRNAs in RNA interference (RNAi) and antiviral defense was initially characterized in model organisms like *Caenorhabditis elegans* and Drosophila melanogaster, providing a foundation for subsequent plant studies. Recent advancements have provided deeper insights into the complexity of sRNA biogenesis and function. High-throughput sequencing technologies have enabled the identification of novel miRNAs and siRNAs in various plant species, revealing a greater diversity of sRNA pathways than previously anticipated. Additionally, the discovery of phased secondary siRNAs (phasiRNAs) has expanded our understanding of how sRNAs can amplify silencing signals. PhasiRNAs are generated from specific precursor transcripts in a phased manner, often triggered by an initial miRNA-guided cleavage event. This amplification mechanism allows for robust and localized gene silencing, playing crucial roles in regulating gene expression in response to environmental and developmental cues. Furthermore, recent studies have highlighted the intricate regulatory networks involving sRNAs and their interactions with other molecular pathways. For example, the interplay between miRNAs and phytohormone signaling pathways has been extensively studied, revealing how sRNAs fine-tune plant responses to biotic and abiotic stresses. The role of siRNAs in transgenerational inheritance of stress responses and epigenetic regulation has also emerged as a significant area of research, demonstrating how plants can pass on acquired resistance to offspring. These advancements underscore the dynamic and multifaceted nature of sRNA-mediated regulation in plants. The detailed understanding of sRNA biogenesis and function not only provides insights into fundamental biological processes but also opens up new avenues for developing innovative strategies for crop improvement. By leveraging sRNA-based approaches, it is possible to enhance disease resistance, stress tolerance, and overall plant productivity, contributing to sustainable agriculture and food security. In summary, the biogenesis of miRNAs and siRNAs involves complex and tightly regulated processes that are essential for their function as gene expression regulators. Advances in high-throughput sequencing and molecular biology techniques have significantly expanded our understanding of these pathways, revealing new layers of complexity and regulation. These insights pave the way for novel applications in plant biotechnology and crop improvement, highlighting the potential of sRNAs as powerful tools for enhancing plant health and productivity.

Comparative studies

Early research laid the groundwork for understanding the basic mechanisms of sRNA biogenesis and function. For instance, Reinhart *et al.* (2002) [7] provided foundational insights into the identification and characterization of miRNAs in *Arabidopsis*. The discovery of Dicer and Argonaute proteins as core components of the RNAi machinery by Bernstein *et al*. (2001) [8] and Hammond *et al*. (2001) [9] respectively, were pivotal in establishing the biochemical pathways involved in sRNA function.

Recent studies have expanded our knowledge by uncovering additional layers of complexity in sRNA biogenesis and function. Advances in high-throughput sequencing technologies have enabled the identification of numerous novel miRNAs and siRNAs across various plant species, revealing a broader diversity of sRNA pathways. For instance, the work of Axtell *et al*. (2011) [10] on phased siRNAs (phasiRNAs) in rice and their role in amplifying gene silencing signals highlighted the sophisticated regulatory capabilities of sRNAs.

Furthermore, the interplay between sRNAs and other regulatory networks, such as hormone signaling pathways and epigenetic modifications, has been increasingly recognized. Research by Li *et al*. (2012) [11] demonstrated how miRNAs interact with salicylic acid (SA) and jasmonic acid (JA) pathways to modulate immune responses, providing a deeper understanding of the crosstalk between different regulatory systems in plants.

Small RNAs in regulating disease resistance in plants

Small RNAs (sRNAs) have emerged as critical regulators of gene expression in plants, playing pivotal roles in orchestrating disease resistance. These sRNAs, including microRNAs (miRNAs) and small interfering RNAs (siRNAs), act by guiding RNA-induced silencing complexes (RISCs) to target messenger RNAs (mRNAs), resulting in mRNA degradation or translational repression. The intricate regulatory networks mediated by sRNAs enable plants to mount effective defense responses against a wide array of pathogens, including bacteria, fungi, viruses, and nematodes.

The role of miRNAs in disease resistance involves the fine-tuning of gene expression related to immune responses. For instance, miRNAs can modulate the levels of resistance (R) genes, which are responsible for recognizing pathogen effectors and activating downstream defense mechanisms. One well-studied example is miR482 and miR2118 in tomato, which target transcripts of nucleotide-binding leucine-rich repeat (NLR) R genes. During pathogen attack, the downregulation of these miRNAs leads to an increase in NLR transcript levels, enhancing the plant's defensive capacity. This regulation is crucial for balancing immune responses to avoid unnecessary energy expenditure and potential autoimmunity.

In comparison, siRNAs primarily function in silencing viral RNA and regulating transposons, but they also play significant roles in plant immunity. For example, the generation of phased siRNAs (phasiRNAs) involves an initial miRNA-triggered cleavage of a precursor RNA, followed by the production of secondary siRNAs in a phased manner. These phasiRNAs amplify the silencing signal and target additional mRNAs involved in defense responses. In rice, phasiRNAs have been shown to regulate genes that negatively control immunity, thereby enhancing resistance to bacterial pathogens.

Previous studies have laid the groundwork for understanding the basic mechanisms of sRNA function in plant immunity. Early research identified several miRNAs and siRNAs involved in stress responses and provided insights into their biogenesis and target recognition. For instance, initial studies in Arabidopsis thaliana demonstrated that miR393 targets transcripts encoding F-box proteins, which are involved in auxin signaling. Upon pathogen infection, the upregulation of miR393 suppresses auxin signaling, thereby prioritizing defense responses over growth.

Recent advancements have further elucidated the complex interactions between sRNAs and other regulatory pathways. High-throughput sequencing technologies have facilitated the discovery of numerous sRNAs and their targets, revealing a broader spectrum of sRNA-mediated regulation than previously known. For example, the interplay between miRNAs and hormonal pathways such as salicylic acid (SA), jasmonic acid (JA), and ethylene (ET) signaling has been extensively studied. These hormones are crucial for modulating immune responses, and their signaling pathways are tightly regulated by miRNAs. The dynamic regulation of hormonal pathways by miRNAs allows plants to fine-tune their defense responses according to the type and intensity of the pathogen attack. Moreover, the role of sRNAs in transgenerational immune priming has emerged as a fascinating area of research. Plants exposed to certain pathogens can pass on acquired resistance traits to their progeny through sRNA-mediated epigenetic modifications. This form of transgenerational memory enhances the ability of subsequent generations to respond more robustly to similar threats, providing an evolutionary advantage. The practical applications of sRNA knowledge in crop improvement have also seen significant progress. Genetic engineering techniques, such as CRISPR-Cas9, have been employed to manipulate sRNA pathways for enhanced disease resistance. For example, CRISPR-Cas9 has been used to knock out miRNA genes that suppress R genes, thereby increasing the expression of R genes and improving resistance to pathogens. Additionally, exogenous application of synthetic sRNAs targeting pathogen genes has shown promise in protecting crops from viral infections. In summary, small RNAs are integral to the regulation of disease resistance in plants, modulating a wide range of genes and pathways involved in immune responses. The advancements in understanding sRNA functions and interactions have significantly expanded our knowledge of plant immunity, highlighting the complexity and sophistication of sRNA-mediated regulation. These insights not only enhance our fundamental understanding of plant biology but also pave the way for innovative strategies in crop protection and improvement, contributing to sustainable agricultural practices and global food security.

Conclusion

Small RNAs (sRNAs) play a pivotal role in regulating disease resistance in plants, acting as master regulators of gene expression and orchestrating complex defense responses. The intricate networks of microRNAs (miRNAs) and small interfering RNAs (siRNAs) modulate the expression of key resistance genes, hormonal pathways, and stress-responsive elements, enabling plants to effectively combat a wide array of pathogens. Advances in high-throughput sequencing and molecular biology have significantly deepened our understanding of sRNA biogenesis and function, revealing new layers of regulatory complexity and interaction. This study has highlighted the dual roles of miRNAs and siRNAs in fine-tuning plant immunity. MiRNAs are crucial for balancing immune responses by regulating resistance genes and hormone signaling pathways, ensuring an effective but controlled defense mechanism. SiRNAs, particularly phased siRNAs, amplify silencing signals and contribute to robust and localized defense responses. The interplay between sRNAs and other regulatory mechanisms underscores the dynamic nature of plant immunity, allowing plants to adapt to diverse and evolving pathogenic threats. Comparisons with previous studies show a significant progression from initial discoveries of sRNAs' involvement in stress responses to a detailed understanding of their specific roles in disease resistance. The identification of new sRNAs and their targets, as well as insights into transgenerational immune priming and epigenetic regulation, represent major advancements in the field. The practical applications of sRNA knowledge, such as genetic engineering for enhanced disease resistance and the exogenous application of synthetic sRNAs, hold great promise for improving crop resilience. These strategies can lead to the development of disease-resistant plant varieties, contributing to sustainable agriculture and food security. In conclusion, sRNAs are integral to plant immunity, providing sophisticated regulatory mechanisms that enhance disease resistance. Continued research into sRNA pathways and their applications will be crucial for developing innovative solutions to agricultural challenges, ensuring crop protection and productivity in the face of growing global demands.

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