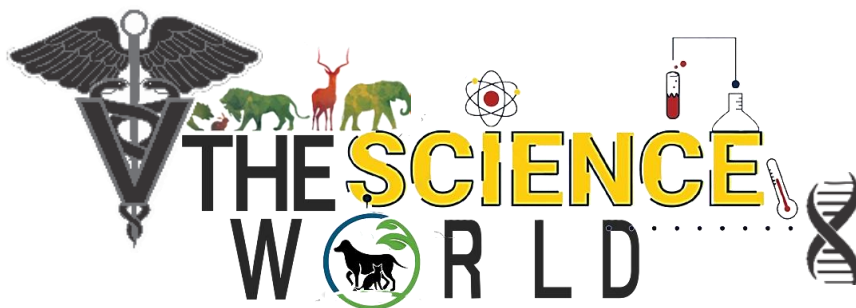




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The Unseen Regulators: How lncRNAs Regulate Plant Responses to Biotic Stress

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Abstract

Long non-coding RNAs (lncRNAs) are RNA transcripts which are longer than 200 nucleotides and do not code for protein, but they are widely recognised as key regulators of gene expression in plants. Unlike microRNAs, lncRNAs act through a diverse range of mechanisms- as decoys and sponges for small RNAs, as scaffolds that recruit chromatin-modifying and transcriptional machinery, as precursors of small RNAs, and even as mobile signals that travel between plant organs. Genome-wide assessments across rice, wheat, tomato, cotton, citrus and several other crops have uncovered thousands of lncRNAs whose expression changes in plants in response to bacterial, fungal, and viral pathogen. An emerging group of these lncRNAs such as ELENA1 in Arabidopsis, ALEX1 in rice, and lncRNA23468 in tomato, among others have been functionally validated and shown to regulate major defense pathways such as salicylic acid and jasmonic acid signalling and NBS-LRR-mediated resistance. This article reviews how lncRNAs are broadening our understanding of plant biotic-stress signalling and why they represent a promising, still largely untapped resource for breeding disease-resilient crops.

Keywords: lncRNAs; Plant Immunity; Biotic Stress; lncRNA-miRNA-mRNA Regulation; Disease Resistance.

INTRODUCTION

High-throughput sequencing of plant genomes has revealed that only a small fraction of the transcribed genome actually codes for protein. The rest is transcribed into non-coding RNAs of many kinds, and among these, long non-coding RNAs (lncRNAs) that are transcripts longer than 200 nucleotides with little or no protein-coding capacity, have emerged as one of the most versatile classes of gene regulators. Plant lncRNAs are markedly less conserved in



sequence than protein-coding genes, are expressed at levels 30- to 60-fold lower than mRNAs, and show strongly tissue and stress specific expression patterns. Most of the lncRNAs are transcribed by RNA Polymerase II in the same manner as protein-coding genes, although the plant-specific Polymerases IV and V also contribute a distinct subset that feeds into small-RNA-mediated silencing pathways. According to their genomic location relative to neighbouring genes, lncRNAs are broadly classified as long intergenic ncRNAs (lincRNAs), natural antisense transcripts (NATs), intronic, and bidirectional or overlapping lncRNAs.

Since plants cannot physically escape pathogens, they depend entirely on molecular defence mechanisms and rapid transcriptional responses for defense. This immune system involves two major layers of defence: pattern-triggered immunity (PTI), activated when cell-surface receptors detect conserved pathogen or microbe-associated molecular patterns, and effector-triggered immunity (ETI), a stronger response mounted when intracellular NB-LRR proteins recognise pathogen effectors that have breached PTI. Both layers have been studied mainly in relation to protein-coding resistance genes, transcription factors and hormone pathways. Over the last decade, however, transcriptome-wide studies have revealed that lncRNAs function as an additional layer alongside these regulators that is a largely hidden layer of regulation, one that determines how strongly, how quickly and how precisely a plant responds to pathogen attack.

HOW lncRNAs WORK

Unlike microRNAs, which function via a single, well-defined mechanism of target cleavage or translational repression, lncRNAs regulate gene expression through several distinct and sometimes overlapping mechanisms.

Decoys and target mimics (ceRNA activity)

Many lncRNAs contain sequence motifs that resemble the binding sites of specific microRNAs. By binding and ‘sponging’ a microRNA without being cleaved themselves, these lncRNAs act as competing endogenous RNAs (ceRNAs) and allowing the microRNA’s target genes to be expressed more freely. The founding example is IPS1 in Arabidopsis, which sequesters miR399 to regulate phosphate-starvation responses (Franco-Zorrilla *et al.*, 2007), a mechanism widely observed in biotic-stress responses. In tomato, lncRNA23468 acts as a target mimic for miR482b, a microRNA that ordinarily represses NBS-LRR resistance genes; by soaking up miR482b, lncRNA23468 allows NBS-LRR transcripts to accumulate and strengthens resistance to the oomycete *Phytophthora infestans* (Jiang *et al.*, 2019).



Protein scaffolds and decoys

Some lncRNAs work by interacting with protein rather than RNA, promoting or interfering with the assembly of transcriptional complexes. The Arabidopsis lncRNA ELENA1 is induced within minutes of perceiving the bacterial elicitor elf18 and physically recruits the transcriptional co-activator MED19a to the promoter of PATHOGENESIS-RELATED GENE 1 (PR1), while simultaneously displacing the repressive protein FIBRILLARIN 2 from the same complex, together driving strong PR1 induction and enhanced resistance to *Pseudomonas syringae* (Seo *et al.*, 2019).

Epigenetic and chromatin-level regulation

Another layer of regulation operates through chromatin. The lncRNA SABC1 in Arabidopsis recruits the Polycomb repressive complex component CURLY LEAF to deposit repressive H3K27me3 marks at the NAC3 locus, keeping salicylic-acid biosynthesis in check under normal conditions; pathogen infection lowers SABC1 levels, releasing NAC3 and boosting salicylic-acid-dependent defense (Liu *et al.*, 2022). This kind of epigenetic mechanism demonstrate how lncRNAs help plants balance the cost of immunity against the cost of growth.

Mobile, long-distance signals

Some lncRNAs are not confined to the cell and can travel & act beyond their cells of origin. Phloem-based transcriptomic studies have found dozens of lncRNAs, including IPS1, moving systemically between roots and shoots in response to nutrient stress, and a distinct signalling role for ELENA1 has been described in root-to-shoot communication during nitrogen deficiency (Fahad *et al.*, 2024). Whether pathogen-responsive lncRNAs use similar long-distance routes to induce systemic acquired resistance remains an important area of research.

lncRNAs IN DEFENSE AGAINST BACTERIAL PATHOGENS

Bacterial pathogens penetrates plant defenses through wounds or natural openings and multiply in the apoplast or xylem, and several lncRNAs have now been tied to the plant response. Besides ELENA1's role against *Pseudomonas syringae* described above, the rice lncRNA ALEX1 is strongly induced upon infection by *Xanthomonas oryzae* pv. *oryzae*, the cause of bacterial leaf blight; ALEX1 activates jasmonic-acid biosynthesis and signalling, raising endogenous jasmonate levels and the expression of JA-responsive defense genes, and its overexpression confers broad-spectrum resistance to bacterial pathogens (Yu *et al.*, 2020). In citrus, comparative transcriptomics of Huanglongbing-affected plants identified thousands of lncRNAs, among which LNC_28805 upregulates the transcription factor WRKY33 and the



syntaxin gene SYP121, two defense genes linked to resistance against *Candidatus Liberibacter asiaticus*, the pathogen responsible for this economically devastating disease (Zhuo *et al.*, 2023).

lncRNAs IN DEFENSE AGAINST FUNGAL AND OOMYCETE PATHOGENS

Fungal and oomycete pathogens are the most damaging biotic stresses that pose major threat to crop yield worldwide, and this is where most of the evidence related to lncRNA has emerged, largely in tomato's interaction with the late-blight oomycete *Phytophthora infestans*. Alongside lncRNA23468 (above), tomato lncRNA16397 induces the glutaredoxin gene SlGRX, curbing the accumulation of reactive oxygen species and membrane damage and thereby improving resistance (Cui *et al.*, 2017), while lncRNA39026 acts as a decoy for miR168a — a microRNA that would otherwise silence the core RNA-silencing component Argonaute1 and in doing so promotes the expression of pathogenesis-related genes (Hou *et al.*, 2020).

In cereals, wheat responding to powdery mildew (*Blumeria graminis* f. sp. *tritici*) expresses several lncRNAs, including TapmlnRNA5, TapmlnRNA8 and TapmlnRNA19, which fold into stable hairpin structures and act as precursors of stress-responsive small RNAs (Das *et al.*, 2023); genome-wide surveys have since catalogued several hundred differentially expressed lncRNAs in wheat challenged by powdery mildew and stripe rust (Zhang *et al.*, 2020). In cotton, GhIncLOX3 positively regulates its neighbouring gene GhLOX3, boosting jasmonic-acid biosynthesis and resistance to *Verticillium dahliae*, while silencing GhIncLOX3 compromises this resistance (Wang *et al.*, 2021). Most of this functional evidence has emerged from a small number of model or high-value dicot crops and a several wheat–fungus pathosystems focused on the biotrophic pathogens powdery mildew and stripe rust.

lncRNAs IN DEFENSE AGAINST VIRAL PATHOGENS

Virus-borne diseases account for roughly half of all plant disease losses worldwide, and lncRNAs contribute to antiviral defense mainly by acting as microRNA decoys or precursors of antiviral small RNAs. In tomato, infection with tomato yellow leaf curl virus (TYLCV) alters the expression of many lncRNAs in a resistant line; among them, slylnc0195 and slylnc1077 function as target mimics that sequester miR166 and miR399 respectively, strengthening resistance (Wang *et al.*, 2015). In maize, sugarcane mosaic virus infection changes the expression of over a hundred lncRNAs; silencing lncRNA10865 increases viral accumulation together with miR166j-3p, whereas silencing lncRNA14234 suppresses the virus and downregulates SPL11, a target of miR394a-5p — evidence that lncRNA–miRNA–mRNA interactions shape the outcome of infection (Gao *et al.*, 2024). The same SABC1-mediated



salicylic-acid module described earlier for bacterial defense also contributes to Arabidopsis resistance against turnip mosaic virus, underlining that individual lncRNAs can operate across more than one class of pathogen (Liu *et al.*, 2022).

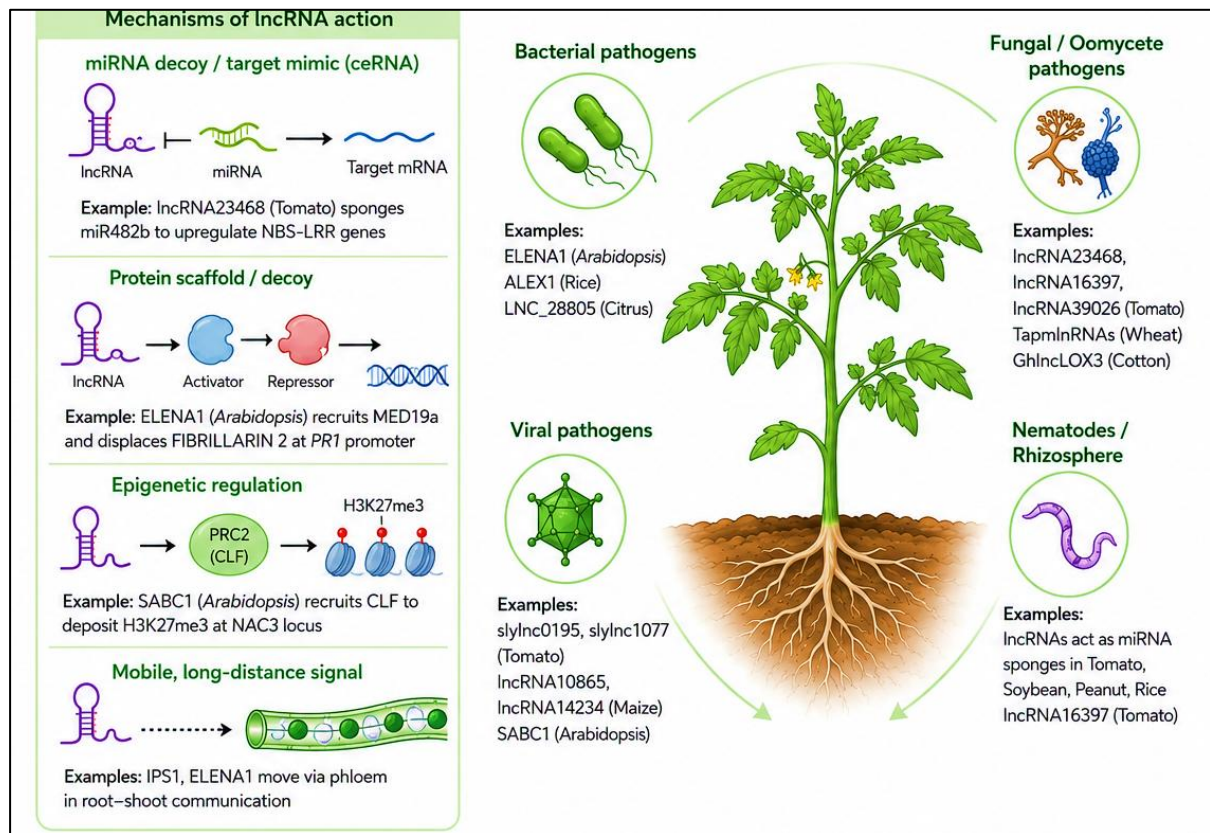


Figure 1. Schematic representation of the molecular mechanisms by which plant lncRNAs regulate responses to diverse biotic stresses and their potential applications in crop disease resistance and improvement.

Beyond The Leaf: Nematodes, The Rhizosphere, And Translational Potential

The rhizosphere is the belowground interface where plant roots interact with diverse soil microbes through the release of exudates. lncRNA profiling in tomato, soybean, peanut and rice has identified differentially expressed lncRNAs that act as microRNA sponges during nematode infection, however most of these are functionally uncharacterised (Fahad *et al.*, 2024). Recent studies have shown that lncRNA expression changes rapidly in response to plant rhizosphere interactions, leading to the activation of defense signaling pathways, such as ROS production or hormone response (Huang *et al.*, 2023). For instance, tomato lncRNA16397 decreases the accumulation of ROS and alleviates damage to cell membranes, thus enhancing resistance to *Phytophthora infestans*, possibly by upregulating the expression of its neighboring gene *SlGRX* (Cui *et al.*, 2017).



lncRNAs have emerged as critical gene-expression regulators that govern plant growth, development, and stress-response processes. However, their roles in mediating plant adaptations at the rhizosphere interface remain poorly defined. Therefore, an urgent and demanding question is how information about lncRNAs can be harnessed in breeding programs, for example by using them as biomarkers for specific traits or leveraging their regulatory roles in rhizosphere signals. We foresee that high-resolution spatial mapping of root lncRNA expression integrated with multi-omics data can provide foundational insights into the complex lncRNA-dependent transcriptional networks that underlie plant–environment interactions. Thus, deciphering the precise lncRNA-dependent networks associated with crop resilience to diverse belowground stresses will ultimately illuminate innovative targets and solutions for sustainable agriculture.

CONCLUSION

lncRNA research in plants is still in its early stage and requires extensive study to fully elucidate their diverse roles in plant immunity, development, disease resistance, and hormone signalling. They act as microRNA decoys, protein scaffolds, chromatin modifiers and even mobile signals, and lncRNA such as ELENA1, ALEX1 and lncRNA23468 show that they can strongly influence plant susceptibility and resistance. While advances in bioinformatics and high-throughput RNA sequencing (RNA-seq) have accelerated the identification of novel lncRNAs, functional characterization remains limited. Current evidence demonstrates that lncRNAs are integral to complex regulatory networks, acting as early modulators of immune signaling pathways, stress responses, and developmental processes. Ultimately, a deeper understanding of lncRNA-mediated immune responses and stress adaptation mechanisms will pave the way for innovative, sustainable strategies to combat plant diseases and secure global food production.

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