



# Harnessing the potential of non-coding RNA: An insight into its mechanism and interaction in plant biotic stress

Syed Muhammad Iqbal Syed Othman<sup>a</sup>, Arif Faisal Mustaffa<sup>a</sup>, Nur Irdina Izzatie Mohd Zahid<sup>a</sup>, M. Hafiz Che-Othman<sup>a</sup>, Abdul Fatah A. Samad<sup>b</sup>, Hoe-Han Goh<sup>c</sup>, Ismanizan Ismail<sup>a,c,\*</sup>

<sup>a</sup> Department of Biological Sciences and Biotechnology, Faculty of Science and Technology, Universiti Kebangsaan Malaysia (UKM), Bangi, 43600, Selangor, Malaysia

<sup>b</sup> Department of Biosciences, Faculty of Science, Universiti Teknologi Malaysia (UTM), Skudai, Johor Bahru, 81310, Johor, Malaysia

<sup>c</sup> Institute of Systems Biology, Universiti Kebangsaan Malaysia (UKM), Bangi, 43600, Selangor, Malaysia

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## ABSTRACT

Plants have developed diverse physical and chemical defence mechanisms to ensure their continued growth and well-being in challenging environments. Plants also have evolved intricate molecular mechanisms to regulate their responses to biotic stress. Non-coding RNA (ncRNA) plays a crucial role in this process that affects the expression or suppression of target transcripts. While there have been numerous reviews on the role of molecules in plant biotic stress, few of them specifically focus on how plant ncRNAs enhance resistance through various mechanisms against different pathogens. In this context, we explored the role of ncRNA in exhibiting responses to biotic stress endogenously as well as cross-kingdom regulation of transcript expression. Furthermore, we address the interplay between ncRNAs, which can act as suppressors, precursors, or regulators of other ncRNAs. We also delve into the regulation of ncRNAs in response to attacks from different organisms, such as bacteria, viruses, fungi, nematodes, oomycetes, and insects. Interestingly, we observed that diverse microorganisms interact with distinct ncRNAs. This intricacy leads us to conclude that each ncRNA serves a specific function in response to individual biotic stimuli. This deeper understanding of the molecular mechanisms involving ncRNAs in response to biotic stresses enhances our knowledge and provides valuable insights for future research in the field of ncRNA, ultimately leading to improvements in plant traits.

## 1. Introduction

Plants possess a sophisticated defence mechanism that enables them to withstand the biotic stress caused by pathogens, including bacteria, viruses, fungi, nematodes, oomycetes, and insects. This intricate system equips plants with the ability to thrive even in the most challenging and unfavourable conditions (Khare et al., 2020). The plant's defence system encompasses both structural and chemical defences, which play integral roles in safeguarding against potential threats. Structural defences, such as thick cuticles, waxy coats, and spines, act as formidable barriers that impede the penetration of pathogens through the plant's surface. On the other hand, chemical defences involve the production of antimicrobial compounds such as phytoalexins, which exhibit toxicity towards pathogens and effectively shield the plant from potential attacks (Wolf, 2022). However, the defence mechanism of plants is influenced by the regulation of multiple genes and regulatory layers in response to

unfavourable environmental conditions (Jan et al., 2021). Understanding these regulatory pathways is crucial for using biotechnology to develop stress-tolerant plants.

Plants have developed several molecular mechanisms to adapt to stressful conditions, including non-coding RNAs (ncRNAs). These ncRNAs do not encode proteins and may constitute a substantial portion of RNA transcripts, accounting for more than 90% of the eukaryotic genome (Xue et al., 2020). ncRNAs play diverse roles in plants, including developmental processes, pathogen defence, insect defence, and responses to environmental cues (Samad et al., 2017; Šečić et al., 2021a). By regulating the expression of pathogenesis-related genes, ncRNAs maintain a delicate balance between plant defence and growth. Maintaining balance allows plants to respond effectively to biotic stress and protect themselves against pathogens. Thus, ncRNAs play a vital role in regulating plant immunity and ensuring plant survival against biotic stresses (Jha et al., 2021). Gaining a deeper understanding of these

\* Corresponding author. Department of Biological Sciences and Biotechnology, Faculty of Science and Technology, Universiti Kebangsaan Malaysia (UKM), Bangi, 43600, Selangor, Malaysia.

E-mail address: [maniz@ukm.edu.my](mailto:maniz@ukm.edu.my) (I. Ismail).

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mechanisms and exploring ncRNA-based approaches may lead to innovative strategies for enhancing plant resistance to biotic stress and agricultural productivity. Therefore, this review emphasises the significance of ncRNAs in inducing resistance and presents evidence of their involvement in encountering various types of biotic stress responses.

## 2. Overview of non-coding RNAs in plants

A comprehensive examination of ncRNAs was conducted using genome-wide scans across various plant species, such as *Arabidopsis* and *Medicago truncatula*. The structure of plant RNA can be categorised into linear ncRNAs and circular ncRNAs (circRNAs). Linear ncRNAs can be divided into two main groups: housekeeping and regulatory ncRNAs. Housekeeping RNAs consist of ribosomal RNAs, transfer RNAs (tRNA), and small nucleolar RNAs, whereas linear ncRNAs are mostly regulatory (Xue et al., 2023). Regulatory ncRNAs can be broadly sorted into two categories based on their length: small ncRNAs (sRNAs) and long ncRNAs (lncRNAs). sRNAs are characterised by their relatively short size, typically under 200 nucleotides. They encompass a variety of small RNA types, including microRNAs (miRNAs), which are approximately 22 nucleotides long; small interfering RNAs (siRNAs), ranging from 20 to 25 nucleotides in length; and PIWI-interacting RNAs (piRNAs), natural antisense short interfering RNA (natsiRNAs), and trans-acting siRNA (tasiRNAs), which vary from 21 to 30 nucleotides in length (Jin et al., 2013).

sRNAs can be divided into two categories: miRNAs and siRNAs. Both types of sRNAs share a standard feature, which is their generation through the activity of enzymes known as Dicers or Dicer-like proteins (DCLs). miRNAs represent an endogenous class of sRNAs that modulate gene expression by targeting distal genes within the genome. They achieve this by exhibiting partial or exact complementarity to their transcript targets (Mengistu and Tenkegna, 2021). Furthermore, miRNAs typically comprise 20–24 nucleotides and are expressed by RNA polymerase II under specific spatiotemporal conditions regulated by plant *MIR* genes. Their role is to control the quantity and accumulation of target messenger RNAs (mRNAs) and indirectly interfere with various plant processes regulated by DCL1. Upon maturation, miRNAs assemble into Argonaute proteins (AGOs) and form RNA-induced silencing complexes (RISCs), which subsequently induce post-transcriptional gene silencing (PTGS) to their target genes (Dong et al., 2022). In contrast, siRNAs are derived from double-stranded RNA (dsRNA) precursors that can arise from diverse sources, such as aberrant transcripts, inverted repeats, ncRNAs, and exogenous RNAs. siRNAs are transcribed by RNA polymerase IV or RNA-dependent RNA polymerases (RDRs) (Hudzik et al., 2020). Subsequently, siRNAs are processed by DCL2 (generating 22 nt), DCL3 (generating 24 nt), and DCL4 (generating 21 nt) from dsRNA and subsequently bind to AGO proteins to form RISCs (Henderson et al., 2006).

In general, lncRNAs are a class of ncRNAs that cannot code for proteins. However, they have a length of more than 200 nucleotides and have limited sequence similarity across species. While RNA polymerase II transcribes most lncRNAs in plants, plant-specific RNA polymerases IV and V also transcribe some lncRNAs. These lncRNAs often exhibit distinct expression patterns and spatial organisation (Wu et al., 2020). Furthermore, lncRNAs are classified into several types: intergenic, intronic, sense, and bidirectional. Intergenic lncRNAs are transcribed from regions of the genome that are not within protein-coding genes but are co-transcribed with other long non-coding RNAs, such as natural antisense transcripts (Ariel et al., 2014). Intronic lncRNAs (lincRNAs) are transcribed from the intronic regions of protein-coding genes. In contrast, lincRNAs also form from the intergenic areas between two protein-coding genes in the genome. Sense lncRNAs overlap with the exons of protein-coding genes in the same or complementary strand or with one or more of their exons. Bidirectional lncRNAs are located near the transcription start site of coding genes and are adjacent to the complementary strand, which is transcribed in the opposite direction

(Chen et al., 2017). In addition, another unique type of ncRNA is circRNA, which forms covalently closed loops. circRNAs differ from linear RNAs because their 5' and 3' ends form a covalent bond from canonical back splicing. Moreover, circRNAs typically range from 200 to 600 base pairs, with only a small percentage longer than 2 kb (Zhang et al., 2020).

## 3. Endogenous ncRNA mechanisms in plant immunity

The plant immune system is a complex biological system that involves various intricate mechanisms. These mechanisms include the production of reactive oxygen species (ROS), gene expression reprogramming (such as the induction of PR genes), and the regulation of plant hormone synthesis and signalling pathways (Cao et al., 2018; Luo et al., 2019; Pogorelko et al., 2014). Notably, many ncRNAs regulate diverse cellular processes and play important roles in both pattern-triggered immunity (PTI) and effector-triggered immunity (ETI) responses.

### 3.1. ncRNA-mediated expression of disease resistance genes

PTI is an intrinsic defence mechanism in plants that operates through the recognition of pathogenic molecular patterns or structures by specific pattern recognition receptors (PRRs) located on the surface of plant cells. These transmembrane proteins detect pathogen-associated molecular patterns (PAMPs) and trigger downstream defence responses. The activation of PTI is a crucial step in the plant immune response, leading to the induction of various defence mechanisms, such as the generation of reactive oxygen species, phytohormones, and antimicrobial compounds to counteract pathogen invasion (Couto and Zipfel, 2016). Interestingly, the regulation of PRRs involves ncRNAs that can regulate PRR expression on the cell membrane. For instance, in *Arabidopsis*, miR172b targets the *TOE1* and *TOE2* mRNAs, which are enzymes that suppress the *FLAGELLIN-SENSITIVE 2* (*FLS2*) promoter, thus expression of miR172b increasing *FLS2* gene transcription (Zou et al., 2018).

Furthermore, pathogens employ effector proteins delivered into host cells to subvert the plant's defensive mechanisms. These effectors disrupt PTI, thereby reducing its effectiveness. However, if pathogens evade PTI, plants activate ETI. During ETI, plants use resistance (R) genes to recognise pathogen effectors, triggering a more robust and quicker immune response. R proteins, predominantly intracellular nucleotide-binding/leucine-rich repeat (NLR) receptors and leucine-rich repeat (LRR) proteins mediate ETI responses in plants (Bialas et al., 2017). Without functional R proteins, effector-triggered susceptibility (ETS) occurs, allowing pathogens to infect susceptible hosts (Bjornson and Zipfel, 2021).

Interestingly, ncRNAs, including lncRNAs and sRNAs, regulate R gene expression. In rice infected with the blast fungus, RNA sequencing showed major transcriptional changes, with 161 lncRNAs being differentially expressed in both upregulated and downregulated. Six of these differentially expressed lncRNAs were validated using reverse transcription-quantitative polymerase chain reaction (RT-qPCR). Comparative analysis of the expression levels between differentially expressed lncRNAs and neighbouring genes suggested their involvement in plant immunity. Most of the 34 differentially expressed lncRNA-gene pairs were positively correlated with host genes, suggesting their potential roles (Wang et al., 2020). Some lncRNAs interact with R genes, PRR genes, and transcription factors (TFs) to regulate the kiwi immune response to *Pseudomonas syringae* pv. *Actinidiae* (Wang et al., 2017b). On the other hand, specific small ncRNAs, such as miR6024, regulate NBS-LRR genes. In tomatoes, miR6024 targets a specific NBS-LRR gene and downregulates its transcript, making the plant susceptible to the *Alternaria solani*. However, the cleavage of the target NLR by miR6024 produces secondary-phased siRNAs, which may enhance defensive signalling and contribute to a necessary defence response (Dey et al., 2022).

### 3.2. ncRNA involved in phytohormone signalling

Plant hormones associated with developmental and abiotic stress responses also respond to biotic defence, including auxin, salicylic acid, jasmonate, and ethylene (Verma et al., 2016). ncRNAs play a pivotal role in governing these reactions. For instance, the inhibition of auxin signalling by the increasing levels of miR393 that suppresses the expression of F-box auxin receptor, *TRANSPORT INHIBITOR RESPONSE 1 (TIR1)* confers resistance to *Verticillium dahliae* in wheat (Shi et al., 2022). Furthermore, miR169 targets the transcription factor *HEME ACTIVATOR PROTEIN 2 (HAP2)*, which binds *HAP3* and *HAP5* to recognise the conserved CCAAT motif in eukaryotic promoters. By negatively regulating *HAP2* expression, miR169 indirectly upregulates the expression of the auxin biosynthesis gene, *INDOLE-3-PYRUVATE MONOOXYGENASE YUCCA2 (YUC2)*, by preventing *HAP2* from binding to its promoter region (Zhang et al., 2017).

In tomatoes, miR166b targets *SIHDZ34* and *SIHDZ45*, class III homeodomain-leucine zipper genes. These genes control the production of jasmonate and ethylene. When the pathogen *Phytophthora infestans* infects a plant, miR166b is activated. This activation lowers the activity of *SIHDZ34/45* and makes the plant more resistant to *P. infestans*. This resistance also involves SI-lncRNA39896 being downregulated when the plant is infected. These findings provide further insights into the complex regulatory role of lncRNAs in plant hormone defence (Hong et al., 2022). Moreover, lncRNAs co-express with jasmonic acid (JA) signalling genes in tobacco plants upon herbivore attack (*Manduca sexta* larvae). The findings showed that up to 1,290 different lncRNA genes were significantly up- or downregulated in response to herbivore treatment, and 1,172 of these lncRNAs were lincRNAs. However, 40 percent of lincRNAs were upregulated, which may be related to late responses to JA expression by *JASMONATE RESISTANCE LONG HYPOCOTYL (JAL)*: *JAL1* and *3* to modulate the abundance of JA expressed high in early responses (Li et al., 2021). A trans-acting lncRNA (lnc\_015092) in *Gossypium hirsutum* targets *LIPOXYGENASE (LOX3)* (*GhlncLOX3*), an enzyme that plays a crucial role in JA biosynthesis. This study revealed the upregulation of *GhlncLOX3*, making the plant more resistant to *V. dahliae* infection. This response suggests that this lncRNA regulates JA production (Wang et al., 2021).

### 3.3. ncRNA involved in ROS regulation

ROS play a crucial role in plant defence against pathogenic microorganisms. However, too much ROS can damage and kill host cells (Yao et al., 2020). Plants have developed various mechanisms to finely regulate ROS levels to maintain a delicate balance between ROS production and scavenging. One mechanism of maintaining ROS homeostasis involves the utilisation of ncRNAs. For instance, overexpression of SI-lncRNA47980 in tomatoes has enhanced their resistance to *P. infestans*. This response was achieved by reducing ROS accumulation and simultaneously elevating JA levels while diminishing gibberellin and salicylic acid production (Su et al., 2023). In Brassicaceae, *FORKED-LIKE7 (FL7)* expression was increased in response to *Phytophthora capsici* infection. However, *BPA1-LIKE PROTEIN3 (BPL3)* suppresses *FL7* and produces cis-natural antisense lncRNA for *FL7 (nalncFL7)*. Moreover, *nalncFL7* also suppresses the *FL7* transcript. The expression of *nalncFL7* coincides with and stabilises the expression of *BPL3*, which negatively regulates ROS during plant biotic responses (Ai et al., 2023). miRNAs have also emerged as key regulators for modulating ROS levels in response to pathogen attacks. For instance, osa-miR398b in rice enhances the activity of superoxide dismutase (SOD) in response to the *Magnaporthe oryzae*, resulting in increased H<sub>2</sub>O<sub>2</sub> concentration and reinforcing the plant's defence against the disease (Li et al., 2019).

### 3.4. ncRNA acting as competing endogenous RNAs (ceRNAs)

Because of unpredictable invasion by pathogens and the complexity

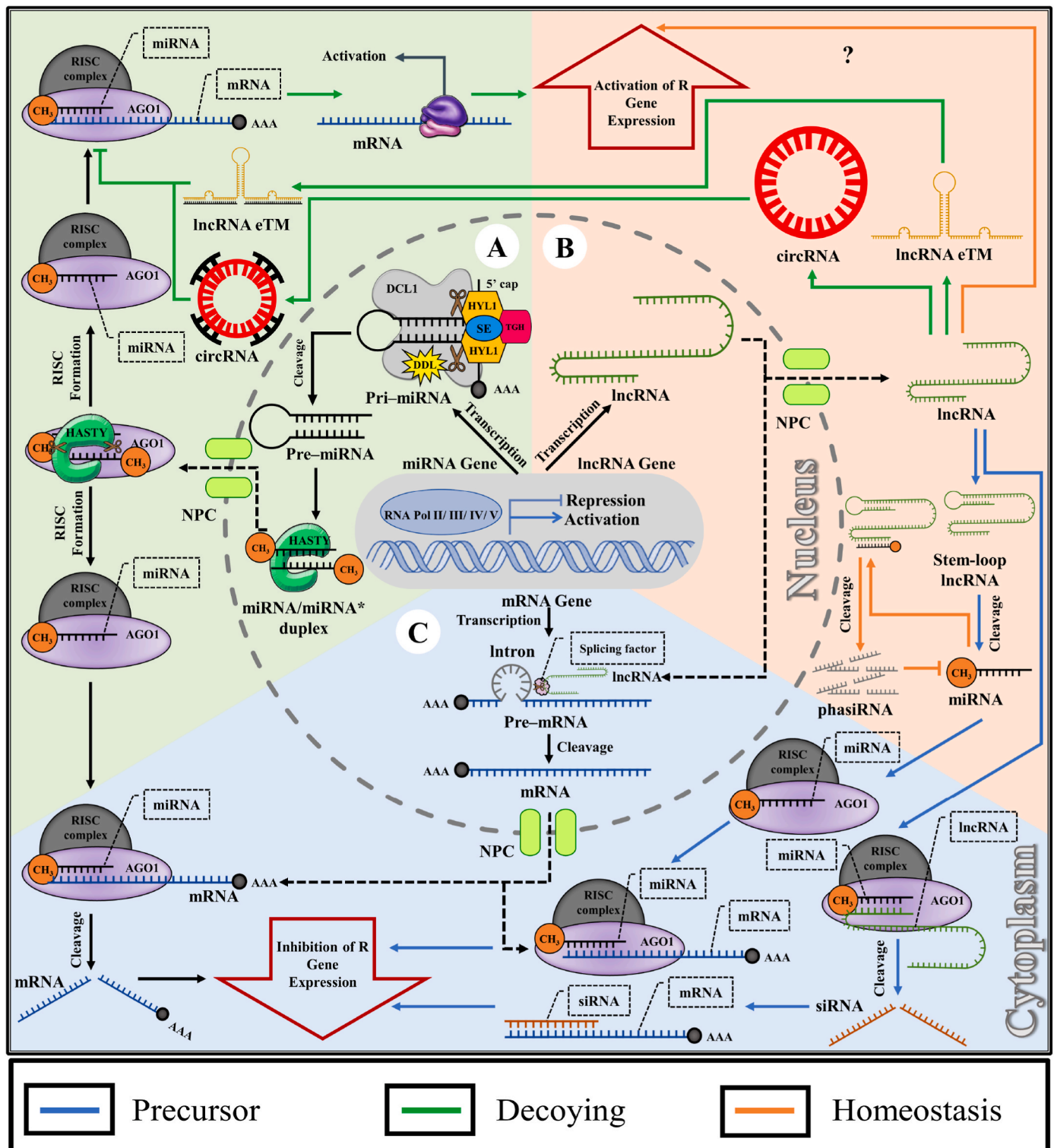
of plant resistance, ncRNAs interact with each other and regulate genes through multiple molecular pathways. To the best of our knowledge, several interconnected interactions have been observed in the action of ncRNAs during plant biotic stress. Here, we found that ncRNA not only suppresses gene-coding transcripts but also interacts with other ncRNA in response to biotic attacks (Fig. 1).

ncRNAs can confer tolerance toward biotic stress through their ability to serve as precursors for other ncRNAs, such as lncRNAs that give rise to miRNAs or siRNAs. For example, XLOC\_006393 is upregulated in virus-tolerant plants as a precursor for NbmiR168c. XLOC\_006393 provides a stem-loop precursor structure cut during alternative splicing (Zheng et al., 2021). Both sRNAs can originate from lncRNAs, which come from other sources besides *MIRNA* genes or small RNA coding genes, and this does not occur only in single lncRNAs in response to biotic stress (Zhang et al., 2014). In mulberry, the lncRNA *MuLnc1* acts as a precursor for siRNA, specifically si161579, which is generated through cleavage by mul-miR3954. This siRNA acts by silencing the calmodulin-like protein gene (*MuCML2*), which plays a vital role in biotic stress responses, thus reducing the plant's ability to adapt to biotic stress. In addition, overexpression of *MuCML27* increased plant tolerance against *Botrytis cinerea* and *P. syringae* tomato DC3000, resulting in more minor spot symptoms in transgenic *Arabidopsis* plants. Conversely, overexpression of si161579 leads to reduced tolerance against both infections (Gai et al., 2018).

In *Arabidopsis*, lncRNAs can serve as sponges for miRNAs during their early stages, thereby inhibiting the cleavage of target mRNAs mediated by the miRNAs. This endogenous competition between ncRNAs demonstrates that lncRNAs can act as decoys for miRNAs, as observed in the case of LNC\_28805, which acts as a decoy for miR5021 when attacked by pathogen (Zhao et al., 2023). Additionally, lincRNAs have been shown to compete with miRNAs in response to infections caused by the *Phytophthora capsica*. The differential expression of lincRNAs leads to the downregulation of miRNAs that target resistance genes, resulting in the upregulation of crucial mRNAs involved in defending against disease (Yin et al., 2021). Moreover, not only lincRNA acts as a decoy for miRNAs, but other lncRNAs also function as target mimics for miRNAs during nematode infections. For instance, in two different nematode species, *Heterodera glycines* (SCN) and *Rotylenchulus reniformis* (RAD), several lncRNAs from RNA sequencing data were annotated as MSTRG.26464.1 in SCN, while MSTRG.2711.1, MSTRG.17076.2, MSTRG.26588.1, and MSTRG.26609.1 in RAD were found to be differentially expressed and act as miRNA mimics in host plants. These lncRNAs downregulate miR156, miR319, and miR396, which are thought to be involved in responding to infection (Khoi et al., 2021). This event also occurs in circRNAs, which act as miRNA sponges. They also bind and mimic the target transcript, effectively decoying miRNAs and preventing them from binding to their intended targets. However, the mechanism of this process in vivo or transgenic plants is not yet fully understood (Sun et al., 2020).

Furthermore, there is evidence of interactions between lncRNAs and miRNAs in both positive and negative regulatory roles, thus maintaining the stability of responses. The application of support vector regression (SVR) identified new target genes in *Arabidopsis*, revealing an intricate pattern of miRNA-lncRNA interactions. miRNAs with low sequence numbers were found to target lncRNAs with high sequence numbers, while miRNAs with high sequence numbers targeted lncRNAs with low sequence numbers. This reciprocal relationship suggests a potential regulatory mechanism where miRNA levels influence lncRNA expression (Bouba et al., 2019). These types of interactions also play a role in plant biotic stress. In the case of *P. infestans* infection, overexpressing lncRNAs in tomatoes increases the accumulation of the resistance gene NBS-LRR. However, excessive accumulation of NBS-LRR leads to the downregulation of lncRNA. Remarkably, SI-lncRNA15492 is downregulated through cleavage by SI-miR482a, which releases SI-lncRNA15492 from suppressing pre-SI-miR482a. This release increases the accumulation of mature SI-miR482a, which removes





**Fig. 1.** Interplay of ncRNA that forms competing endogenous RNAs (ceRNAs) interaction in plant biotic stress. ncRNAs demonstrate a bifunctional role encompassing the repression of gene-coding transcripts as well as complex mechanisms including functioning as decoys, serving as precursors, and preserving homeostasis with other ncRNAs in response to biotic stresses. ceRNAs play a significant role by regulating (A) miRNA, (B) lncRNA, and (C) mRNA expression in the nucleus and cytoplasm. The dotted arrow shows the expression of RNA from the nucleus, whereas the solid arrow indicates the ceRNA mechanism in the cytoplasm. Blunt-head arrows represent inhibition, while pointed-head arrows indicate activation. Arrow lines in blue represent precursors, green represent decoys, and orange represent homeostasis, visually depicting the interaction mechanisms of RNAs within the molecular pathway. The dotted circle is the nuclear membrane, and the green pores are the nuclear pore complex (NPC). Abbreviations: mRNA, messenger RNA; miRNA, microRNA; lncRNA, long non-coding RNA; AGO, Argonaute; siRNA, small interfering RNA; phasiRNA, phased secondary small interfering RNA; eTM, endogenous target mimic; circRNA, circular RNA; RISC, RNA-induced silencing complex.

inhibitory activity and potentially contributes to the formation of phased secondary small interfering RNAs (phasiRNAs) targeting the same sequence as miR482a targets within the pre-SI-miR482a inside the SI-lncRNA15492 antisense sequence (Jiang et al., 2020). Therefore, SI-lncRNA15492 can also inhibit SI-miR482a by increasing its expression, thus maintaining SI-NBS-LRR homeostasis. The interplay between SI-lncRNA15492 and SI-miR482a is essential for maintaining this homeostasis (Jiang et al., 2020). Pathogen- or plant-derived transcripts can potentially disrupt this homeostasis by inhibiting one of the ncRNAs, which can lead to the activation of resistance genes.

#### 4. Cross-kingdom ncRNA mechanisms in plant-microbe interaction

ncRNAs have been shown to move between organisms, even evolutionarily distant ones, regulating gene expression in other organisms. An essential factor in cross-kingdom communication involves the release of extracellular vesicles (EVs) from the Golgi apparatus. EVs carry various cargoes, including proteins, lipids, coding RNAs, non-coding RNAs, and other molecules (Rutter and Innes, 2018). It is noteworthy that ncRNAs exhibit excellent stability and transferability between kingdoms due to factors such as methylation, interactions with RNA binding proteins, and packaging into exosomes. circRNAs are also stable outside cells due to RNA binding proteins and m<sup>6</sup>A modification. However, ncRNAs can also be transferred outside EVs by binding to proteins (Karimi et al., 2022). In addition, ncRNA transfer occurs during various interactions, such as those between hosts and pathogens and between hosts and symbiotic or mutualistic organisms. ncRNA transfer can suppress pathogen growth or promote mutualistic relationships, both of which have significant effects (Gualtieri et al., 2020). While the precise mechanisms for the cross-kingdom roles of lncRNAs and circRNAs in plant biotic stress remain under investigation, their potential for intercellular and extracellular transfer suggests an influence on plant defence mechanisms (Karimi et al., 2022).

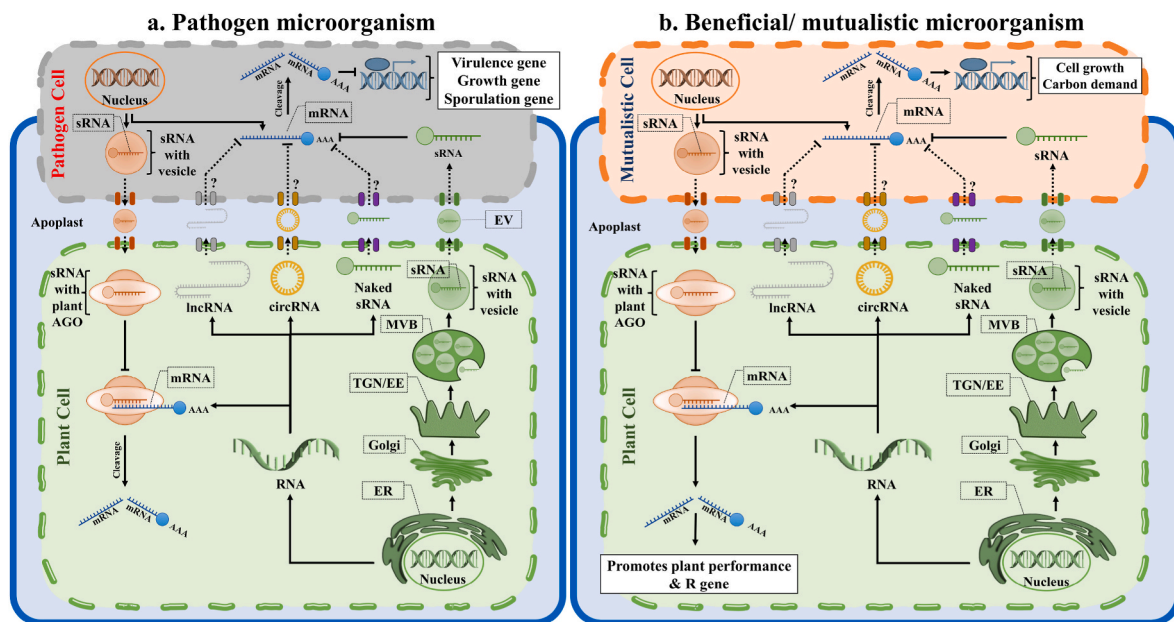
##### 4.1. Cross-kingdom ncRNA transfer between plant and pathogen

The regulatory influence of ncRNAs extends beyond the organism in which they are produced. In the context of plant defence responses, plant hosts can export ncRNAs into pathogens to silence their virulence genes (Zhang et al., 2016). Here, we summarise the defence mechanisms involving sRNA (Fig. 2A).

For instance, cotton plants transport miR166 and miR159 to the hyphae of the *V. dahliae* bacterium, resulting in enhanced disease resistance by downregulating the *PROTEASE (Clp-1)* and *ISO-TRICHODERMIN C-15 HYDROXYLASE (HiC-15)* genes (Zhang et al., 2016). Similarly, transgenic lettuce plants that carried siRNAs that targeted the *HIGHLY ABUNDANT MESSAGE #34 (HAM34)* or *CELLULOSE SYNTHASE (CES1)* genes of the fungal pathogen *Bremia lactucae* had their gene expression greatly reduced. This suppression helps prevent spore formation and fungal growth (Govindarajulu et al., 2015). Furthermore, inter-kingdom transfer of sRNAs has been observed in tomato plants infected with *Botrytis cinerea*. Among the identified sRNAs were miR396a-5p and two siRNAs (siR3 and siR14). These were found in both infected tomato leaves and the pathogen using RT-qPCR. These sRNAs were found to reduce spore germination and subsequently decrease the virulence level of pathogen-induced symptoms (Wu et al., 2023).

##### 4.2. Cross-kingdom ncRNA transfer between plants and beneficial microorganisms

The movement of ncRNA between kingdoms in mutualistic or symbiotic interactions significantly affects how organisms interact with each other and the growth and development of crops as a whole (Gualtieri et al., 2020). So far, sRNA has been found to play a greater role in these interactions than lncRNA or circRNA (Fig. 2B). Previous research has revealed the positive impact of the beneficial fungus *Serendipita indica* (Si) on the growth of *Brachypodium distachyon* (Bd). Upon infection with



**Fig. 2.** Interaction between plants and microbes with ncRNA has positive and negative effects on plants. (A) Plants have a defence strategy against pathogenic microorganisms in which they distribute various types of ncRNAs. These RNAs play a role in inhibiting the expression of genes related to virulence, growth, and sporulation in the pathogens. (B) Microorganisms that provide benefits to plants engage in a mutual relationship where certain mutualistic organisms can capitalise on amplified cellular growth and an elevated demand for carbon resources. Dotted lines represent cell membranes, with the plant cell membrane in green, the pathogen membrane in grey, the mutualistic microorganism membrane in orange, and the blue lines representing cell walls. The solid arrow indicates RNA's movement in the host cell, while the dotted arrow indicates the movement of RNA into other cells. Pointed-head arrows indicate positive regulation, while blunted-head arrows indicate negative regulation. Abbreviations: ER, endoplasmic reticulum; TGN, trans-Golgi network; EE, early endosome; MVB, Multivesicular body; sRNA, small RNA; EV, extracellular vesicle; mRNA, messenger RNA; AGO, Argonaute; lncRNA, long non-coding RNA; circRNA, circular RNA; R gene, resistance gene.

Si, Bd significantly improved grain filling, total grain weight, and shoot length. Interestingly, sRNAs from both the host and the fungus changed the expression found using differentially expressed genes (DEGs). On the other hand, plant miRNAs helped Si cells grow, and Si RNAs helped Bd make flowers better and turn on immune response genes related to pathogenesis (Šečić et al., 2021b). The mutualistic interaction of the *Pisolithus microcarpus* fungus demonstrated the transfer of fungus-derived miRNA, namely PmicmiR-8, when infecting *Eucalyptus grandis* plant roots. This miRNA is transported to the plant roots. It targeted the host NB-ARC domain transcript, which promoted root colonisation without hindering the root development. This symbiotic mechanism can enhance a plant's ability to withstand biotic stress, as the transfer of RNA between different kingdoms often regulates the activation of plant CC-NLR transcripts and R genes (Wong-Bajracharya et al., 2022).

## 5. Role of ncRNAs against various pathogen attacks

ncRNAs play an important role in protecting plants from various pathogens. The role of ncRNAs in the resistance towards pathogens includes regulating gene expression, silencing pathogen genes, triggering immune responses, and acting as decoys. However, plant ncRNAs exhibit specificity in their responses to biotic stress. This specificity arises from distinct mechanisms of action tailored to different pathogens, involving the regulation of genes crucial for various biological processes. Furthermore, plants produce distinct types of ncRNAs in response to specific pathogens. For instance, studies have shown that the tomato plant produces miR166b to counter oomycete attacks but produces miR319 to combat viral infections (Hong et al., 2022; Sharma and Prasad, 2020). The specificity of ncRNAs in plant-pathogen interactions is further highlighted by the differential effects of ncRNA expression on resistance in different pathogens. For example, while overexpression of miR398b in rice confers resistance to fungal *M. oryzae* infection, it simultaneously renders the plant more susceptible to bacterial *P. syringae* infection in *Arabidopsis* (Li et al., 2010, 2014). These findings suggest that ncRNAs regulate plant-pathogen interactions in a pathogen-specific manner. Fig. 3 summarises the role of ncRNAs in responses to different kinds of pathogens (Huang et al., 2023; Song et al., 2021).

Controlling resistance gene networks through ncRNA is important for targeted and effective responses to different biotic stressors. The complex interactions between ncRNAs and protein-coding genes make pathogen-plant interactions complicated, which turn on different sets of genes. The following subsections describe several instances of ncRNAs from different pathogens that enhance plant disease resistance or tolerance.

### 5.1. Fungal

Fungi are eukaryotic pathogens that can cause severe crop diseases, resulting in significant yield losses. ncRNAs regulate plant responses to fungal infections, especially in response to infections caused by diverse fungal species. A genome-wide computational analysis of the oil palm species (*Elaeis guineensis*) revealed the presence of more than 217 miRNAs, which are anticipated to serve as regulators of plant resistance and could be further explored in the context of fungal infections in oil palm (Othman et al., 2022). Among these miRNAs, miR397 has been shown to play a role in responding to fungal infections caused by *V. dahliae*. For instance, miR397 cleaves the laccase gene (*LAC4*), a crucial gene in plant lignin biosynthesis. Therefore, when miR397 is downregulated, it leads to an increase in the abundance of *LAC4*. This increase in *LAC4* abundance also contributes to increased lignin content and plant resistance to fungal infections (Wei et al., 2021). Supporting the involvement of miRNAs in fungal infections, using RNA-seq analysis demonstrated that eight specific miRNAs (miR156, miR158, miR159, miR168, miR169, miR172, miR319, and miR396) exhibited modulated

expression patterns in response to the presence of the leaf rust resistance gene, namely *Lr28*. Moreover, the *Lr28* gene also regulated other downstream resistance pathways, including peroxidases, sugar transporters, auxin response signalling, oxidation-reduction processes, and others (Jain et al., 2023). Previously, miR159 has been shown to play a role in responding to fungal infections, potentially regulating the MYB33 transcription factor in wheat. However, the downstream responses have not been investigated (Salamon et al., 2021).

Furthermore, lncRNAs have also been implicated in regulating diseases caused by fungal pathogens, such as *V. dahliae*. In cotton, two specific lncRNAs, lncNAT XLOC\_051276, and lncNAT XLOC\_002524 regulate resistance to these fungal infections. These lncRNAs are closely associated with gene-code pairing and hormone pathway genes involved in resistance responses. Notably, silencing both lncRNAs enhances resistance to this fungal pathogen (Zhang et al., 2018). Additionally, lncRNA7 and lncRNA2, along with their respective regulatory genes, *PECTIN METHYLESTERASE INHIBITOR 13* (*GbPMEI13*) and *POLY-GALACTURONASE 12* (*GbPG12*), play pivotal roles in fungal infection. lncRNA7 and *GbPMEI13* positively regulate disease resistance, while lncRNA2 and *GbPG12* negatively impact the plant's disease resistance. lncRNA7, encoding the plant peptide phytosulfokine (PSK- $\alpha$ ), triggers the accumulation of 3-indoleacetic acid (IAA) and activates *GbPMEI13* expression through the Auxin Response Factor 5. It's crucial to note that *GbPMEI13* can function as a suppressor of *PECTIN METHYL ESTERASE* (*PME*), an enzyme responsible for modifying cell wall structure. This action potentially aids in protecting the plant cell wall during infection, thereby increasing resistance (Zhang et al., 2022).

### 5.2. Bacteria

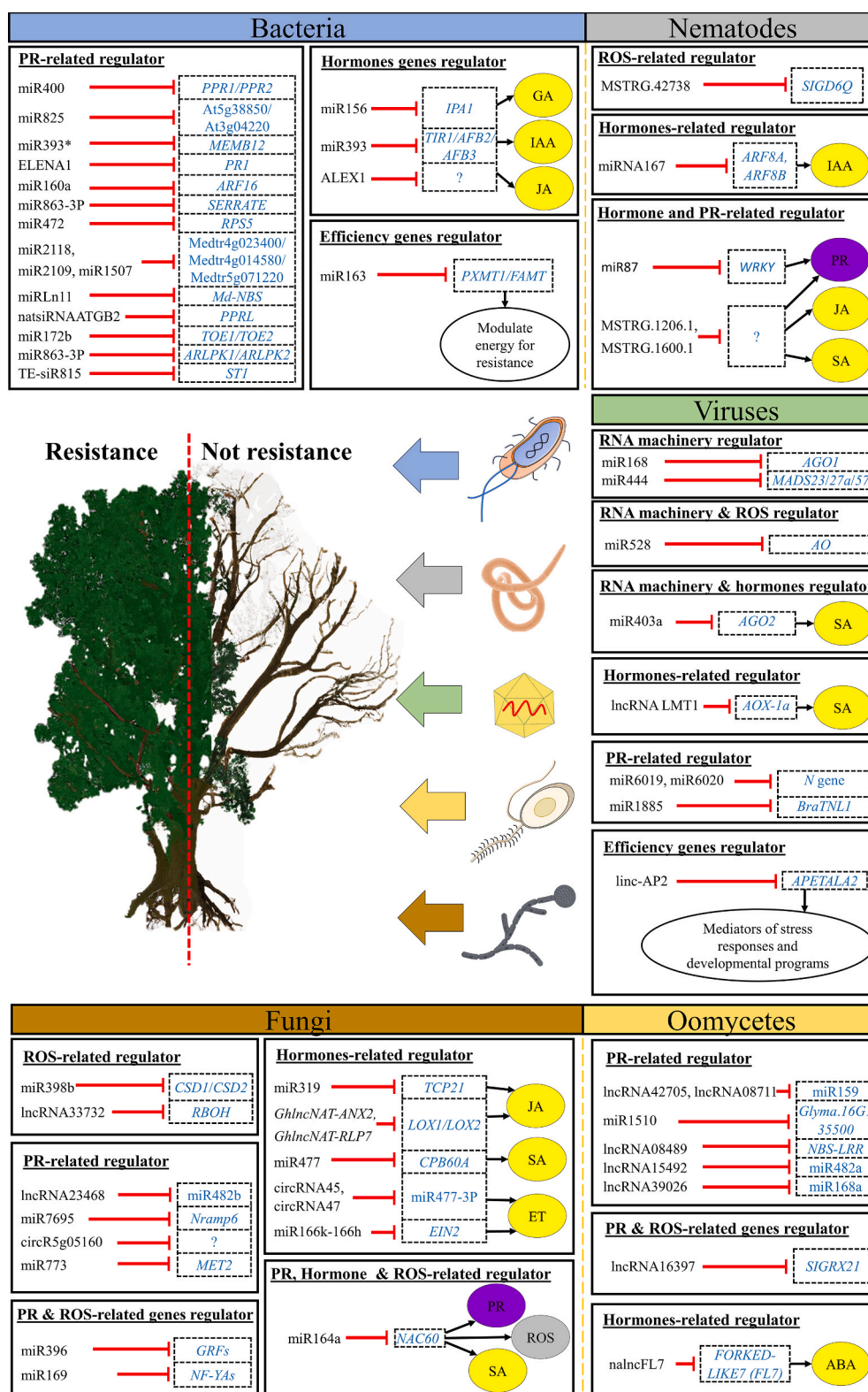
Although bacteria have a seemingly simple structure, they exhibit remarkable diversity on our planet and can have positive and negative effects. Bacteria typically enter the plant root through wounds, root tips, and other infiltration sites and then travel along the root cortex to colonise the vascular system (Digonnet et al., 2012). In the case of *Arabidopsis*, leaf lesions caused by *Pseudomonas syringae* trigger plant protection by increasing the proline content. This increase occurred through the upregulation of proline biosynthesis. Upregulation of proline was made possible by the increased expression of the *1-PYRROLIN-5-CARBOXYLATE SYNTHASE 1* (*AtP5CS1*) transcript, a miRNA164c target. Downregulating miRNA164c raises the expression of *AtP5CS1*, which makes the plant more resistant to bacterial infection (Gupta et al., 2020).

lncRNA has also been studied in citrus plants that respond to the Huanglongbing (HLB) disease caused by the *Candidatus Liberibacter asiaticus* (CLAs) bacteria. A comparative analysis between infected and non-infected plants revealed 8,742 lncRNAs, including 2,529 novel ones, some correlated with HLB. Among these lncRNAs, LNC28805 emerged as a crucial regulator of plant defence genes, upregulating the mRNA transcripts of transcription factor (*WRKY33*) and the syntaxin of plant (*SYP121*), thereby modulating their expression and enhancing plant resistance to HLB (Zhuo et al., 2023). In *Arabidopsis*, the lncRNA *SALICYLIC ACID BIOGENESIS CONTROLLER 1* (*SABC1*) suppresses resistance genes but promotes plant growth when there is no infection. Reducing the levels of this lncRNA improves plant resistance (Liu et al., 2022).

### 5.3. Viruses

Tomato plants infected with the tomato leaf curl virus (ToLCV) exhibit irregular curling of leaves. Specific open reading frames (ORFs) in the viral genome, namely *AC1* (replication-associated protein/Rep), *AC2* (transcriptional activator protein/TrAP), *AC3* (replication enhancer protein/REN), *AC4* (silencing suppressor protein), *AV1* (coat protein/CP), and *AV2* (pathogenicity determinant), affect the pathogenicity of this infection. Each ORF performs distinct functions. For example, *AC2*





**Fig. 3.** List of ncRNAs and their targets in plants' different biotic stress response pathways. ncRNAs specifically target various genes in different biotic stress response pathways, thereby regulating multiple plant immune responses. The red blunted-head arrow indicates negative regulation, while the black pointed-head arrow indicates positive regulation. The blue font with a dotted square represents the transcript targeted by ncRNA, either mRNA or other ncRNAs. The yellow dotted line differentiates ncRNA in different pathogens, while the red dotted line shows the phenotype of infected resistance and non-resistance plants. The coloured circle indicates the response pathway with pathogenesis-related genes in purple, the reactive oxygen system in grey and all hormone responses in yellow. Abbreviations: PR, pathogenesis-related genes; ROS, reactive oxygen species; JA, jasmonic acid; SA, salicylic acid; ABA, abscisic acid; ET, ethylene; GA, gibberellin acid; IAA, 3-indoleacetic acid.

has been found to downregulate the abundance of miR319 and miR172 during *ToLCV* infection (Kumar and Naqvi, 2016). Interestingly, an artificial miRNA based on miR319a has been developed and shown to reduce the pathogenicity of the virus by targeting the ATP/GTP binding domain of *AC1*, thereby regulating viral activity and providing resistance to the plant (Sharma and Prasad, 2020).

Furthermore, lncRNAs regulate plant viruses, such as the Chinese wheat mosaic virus (CWMV) in *Nicotiana benthamiana*. A study identified 65 lncRNAs differentially expressed in infected and non-infected plants including 42 and 23 up- and down-regulated lncRNAs, respectively. Notably, one specific lncRNA, named XLOC\_006393 was found to play a significant role in these responses. Overexpression of XLOC\_006393 resulted in milder symptoms compared to its silencing when infected with CWMV (Zheng et al., 2021).

#### 5.4. Nematodes

Nematodes are recognised as highly destructive pests that pose a significant threat to soil-grown crops. The resistant cultivar Huipizhi (HPZ) and the susceptible cultivar Williams 82 (W82) were studied in soybeans. They had different resistance levels to the soybean cyst nematode (SCN) infection. sRNA libraries were created to analyse miRNAs' differential expression (DE) profiles. Interestingly, the W82 susceptible cultivar correlated with gma-408a expression, while the SCN-resistant HPZ cultivar regulated miRNA expression in response to gma-4994-5p. These findings suggest that both miRNAs may contribute to the plant's defence against nematodes (Lei et al., 2019).

Furthermore, lncRNA also plays a significant role in the defence of plants against nematode infection. In tobacco plants, for example, root-knot nematodes (RKN) substantially impact host lncRNAs, resulting in the differential expression of over 565 lncRNAs under nematode stress. Gene ontology (GO) showed that these lncRNAs were functionally associated with mRNAs that play a part in the plant-nematode response. These lncRNAs have cis-regulatory relationships with genes that play a part in induced systemic resistance, oxidative stress response, hypersensitive response, plant cell wall organisation, DNA binding transcription factor activity, peroxidase activity, and hydrogen peroxide catabolic processes (Li et al., 2018a).

#### 5.5. Oomycetes

Oomycetes, classified within the kingdom Stramenopila, are eukaryotic fungal-like microorganisms that share an evolutionary relationship with algae. In tomatoes, specific sRNAs, particularly miR166b, play a role in regulating resistance against oomycetes. miR166b targets class III homeodomain-leucine zipper genes (*SIHDZ34* and *SIHDZ45*). Moreover, the overexpression of miR166b enhances resistance by increasing levels of JA and ethylene (Hong et al., 2022).

In addition, lncRNA also functions in response to oomycetes. For example, Sl-lncRNA15492 which positively regulates NBS-LRR genes. Overexpression of Sl-lncRNA15492 in plants infected with *P. infestans* results in significantly milder symptoms compared to wild-type plants (Jiang et al., 2020). The tomato WRKY1 transcription factor functions as a positive regulator during *P. infestans* attacks by activating the expression of lncRNA33732. This lncRNA induces *RESPIRATORY BURST OXIDASE (RBOH)*, which leads to increased H<sub>2</sub>O<sub>2</sub> accumulation during the early defence response of tomatoes against *P. infestans* attack (Cui et al., 2019).

### 6. Role of ncRNA against herbivore insects

Insects represent the largest group within the Arthropoda phylum and can inflict damage upon plants through gnawing, sucking, or cutting actions, often associated with egg-laying. Extensive research has been conducted to investigate how plants respond to these stressors. Direct defence mechanisms employed by plants involve physical attributes

such as hairs, trichomes, spines, thorns, and synthesising secondary metabolites, which deter or eliminate insect pests. On the other hand, indirect defence mechanisms encompass the emission of volatile compounds that attract herbivore predators or improve food resource availability for predator populations (War et al., 2018). Plants also possess chemical defence mechanisms that bolster their tolerance against insect attacks. Among these mechanisms, a diverse array of specialised secondary metabolites, including cyanogenic glycosides, gossypol, alkaloids, saponins, and phytoecdysteroids, exert insecticidal effects (Gleadow and Møller, 2014). When cyanogenic glycosides undergo hydrolysis, hydrogen cyanides are released, which block the respiration system and are toxic to insects and mammals. Gossypol, a sesquiterpene aldehyde, can interact with proteins, hindering protease and amylase activities and influencing larval weight gain. Alkaloids like nicotine disrupt insect nervous systems by binding to nicotine acetylcholine receptors. Saponins can induce membrane disruption through pore and vesicle formation. Phytoecdysteroids disrupt insect development by binding to the ecdysone receptor (Gleadow and Møller, 2014). Considering all the findings, ncRNAs play a part in plant defence mechanisms and a regulatory role in determining the levels of secondary metabolites, which also exhibit cross-kingdom RNA effects.

Overexpressing miR396 (OEmiR396) in rice can effectively reduce brown planthopper (BPH) populations by making rice plants much more resistant to BPH. A key target of miR396 is the *GROWTH REGULATING FACTOR 8* (*OsGRF8*), a transcription factor that directly regulates the *flavanone 3-hydroxylase* (*OsF3H*) gene in the flavonoid biosynthesis pathway. This regulatory response is specifically triggered by BPH infestation, leading to an augmented accumulation of flavonoids as a chemical defence mechanism in rice plants (Dai et al., 2019). In addition to miR396, the lncRNA MSTRG.22175 was identified as a contributor to BPH resistance in rice. Comparative analysis of two rice varieties, KW (susceptible to BPH) and KW-Bph36-NIL (NIL) (resistant to BPH), revealed higher expression levels of MSTRG.22175 in the NIL variety. Notably, MSTRG.22175 expression of exons was associated with resistance gene and secondary metabolite expression. The upregulation of MSTRG.22175 mediates the expression of the *Os1lg0303400* gene, resulting in resistance against BPH infestation. Conversely, KW has lower expression levels of MSTRG.22175 (Xue et al., 2023).

Furthermore, several studies proved that sRNAs can be transferred between different kingdoms, including the interaction between plants and insects. Plant miRNAs can travel from plants to animals and interact with their targets, putatively leading to the modulation of gene expression in the recipient (Li et al., 2018b). This evidence has also been observed for miRNA transfer to insect recipients when they feed on plants. For instance, in aphids that attack sorghum, researchers identified over 13 sorghum-derived candidate miRNAs in the aphid *Schizaphis graminum* (Rondani) (GB). Indeed, these miRNAs have the potential to target a total of 16,549 genes that were identified in the aphid genome (Wang et al., 2017a).

### 7. The prospects of ncRNA in enhancing plant defence against biotic stress

ncRNAs play a crucial role in plant defence systems against biotic stressors, including fungal, bacterial, viral, nematode, herbivore, and insect pathogens. Their regulatory mechanisms activate resistance genes and promote RNA movement to inhibit pathogen virulence, highlighting the significance of ncRNAs in plant immune responses. This review focuses on the large body of evidence on the roles of lncRNAs and sRNAs in plant biotic stress responses. In addition, the functions of other ncRNAs that are available from genome sequences, such as tRNA-derived small RNAs (tsRNAs) and circRNAs, in these responses have yet to be fully understood. Recent studies and bioinformatic tools suggest that both tsRNAs and circRNAs also have many regulatory roles in gene expression and likely play important roles in biotic stress regulation (Kalwan et al., 2023; Wang et al., 2023). Moreover, circRNAs originate from various



sources of RNA through back splicing. At the same time, tsRNAs were derived from tRNAs and functioned as regulatory ncRNAs after the cleavage of pre-tRNAs by RNase Z during processing. Despite their potential interactions with other ncRNAs, particularly in biotic stress, the biogenesis and mechanisms of action of these molecules are complex (Wang et al., 2023; Zahra et al., 2023). However, as more crop plant genomes become available, comparative genome analysis allows the study of different ncRNA functions based on sequence similarity and functional annotation across species to identify new ncRNAs for improving plant biotic resistance (Jha et al., 2020).

In addition, various user-friendly tools can be used with a wide range of plant species to investigate ncRNA function, including the continuous, spatial, or temporal expression patterns of ncRNAs in experimental settings by manipulating their promoters. These tools include short tandem target mimicry (STTM), primarily used to control the activities of sRNAs by forming secondary structure RNA that blocks the action of mature miRNAs. miRNA will bind to STTM more than their target transcript, thus increasing the expression of the transcript (Othman et al., 2023). On the other hand, overexpressing ncRNA has also been used to elucidate its function. Surprisingly, overexpressing ncRNA affects endogenous cells within the organism and confers cross-kingdom resistance against biotic attack by entering the cells of other hosts. For instance, in transgenic rice with overexpression of miR162a (OEmiR162a), cross-kingdom RNA interference (RNAi) occurs by targeting the NITOR (target of rapamycin) gene of the Brown Planthopper (BPH), which regulates the insect's reproduction process. Interestingly, this transgenic approach does not affect the plant's morphology but significantly increases its resistance to BPH (Shen et al., 2021).

Moreover, genome editing has been used to improve various plant traits, including biotic resistance, but its use to manipulate ncRNAs is still limited. CRISPR (Clustered Regularly Interspaced Short Palindromic Repeats) is a powerful genome editing tool that can permanently alter plant genomes, enabling gene knockout or knock-in, including modifications for disease resistance (Zhang et al., 2019). For instance, in tomatoes infected with chickpea chlorotic dwarf virus (CpCDV), CRISPR/Cas9 technology was employed to target conserved genomic regions, resulting in mild leaf yellowing, thickened veins and ultimately recovered within 21 days post-infection (Malik et al., 2023). This technology holds the potential to be a novel tool for developing disease-resistant plant traits by controlling ncRNAs. CRISPR/Cas9 could be applied to change the genome by knocking in new ncRNA so that the plant can produce new ncRNAs that can recognise and attack pathogen effectors that the plant would not usually be able to identify. Alternatively, CRISPR/Cas9 could change or remove ncRNAs that are targeted by ncRNAs or proteins from pathogens. This would make it harder for the pathogens to infect plants. In addition, recently, CRISPR/Cas13, which is a CRISPR system that can target RNA, has been applied in plants by splicing mRNA. This mechanism can target ncRNA from either the pathogen or the plant itself to enhance plant resistance when a pathogen attacks (Zhu et al., 2020). Despite limited applications of CRISPR to ncRNAs in plant biotic stress studies thus far, genome editing holds immense promise for enhancing plant resistance through ncRNA manipulation.

Additionally, spray-induced gene silencing (SIGS) using encapsulated RNA or double-stranded RNA (dsRNA) can also be employed as an enhanced defence mechanism against biotic attacks from external sources. A recent development involves the application of dsRNA through leaf spraying, which has shown promising results in protecting against the Y virus infection. The optimal dosage has been achieved by targeting the cp gene of the tomato mosaic virus (ToMV). However, further optimisation of this method is required because dsRNA does not move systemically within the plant and is still ineffective against phloem infections. The mechanism of RNA transfer in this context also remains unclear (Rego-Machado et al., 2020). In addition, the variations in dsRNA uptake efficiencies across microbe species and cell types contribute to the current limitations of SIGS in plant disease

management (Qiao et al., 2021).

## 8. Conclusion

Plant ncRNAs play a significant role in regulating biotic stress responses by inhibiting or activating gene expression in the host or even across different kingdoms. These regulatory mechanisms allow plants to adjust their responses to biotic stress caused by pathogens, pests, and other biotic stressors. Moreover, a single ncRNA has the potential to regulate multiple transcripts and genes, enabling it to respond to different types of attacks with a single ncRNA manipulation or even a single ncRNA being specific to a particular attack. However, the manipulation of ncRNAs can have drawbacks because ncRNAs interactions with other ncRNAs and disease-resistance genes are complex. The manipulation of one ncRNA may exhibit resistance to one pathogen but also increase susceptibility to another pathogen. Further studies are needed to investigate the modulation and functions of ncRNAs. Computational biology and transcriptome sequencing will facilitate the identification and characterisation of unknown ncRNAs. In addition, transgenic and genome editing plants offer promising approaches to studying the loss or gain-of-function of ncRNAs, which could elucidate their functions and enable the development of SIGS for plant disease control. ncRNAs as crucial regulators of plant disease resistance mechanisms present an exciting field of research since developing effective strategies to enhance plant resistance to diseases is essential for ensuring global food security.

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## CRediT authorship contribution statement

**Syed Muhammad Iqbal Syed Othman:** Writing – original draft, Writing – review & editing, Conceptualization, Visualization. **Arif Faisal Mustafa:** Conceptualization, Visualization. **Nur Irdina Izzatie Mohd Zahid:** Conceptualization, Writing – review & editing. **M. Hafiz Che-Othman:** Supervision, Writing – review & editing. **Abdul Fatah A. Samad:** Writing – original draft, Writing – review & editing. **Hoe-Han Goh:** Supervision, Writing – review & editing. **Ismanizan Ismail:** Supervision, Writing – original draft, Writing – review & editing.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

No data was used for the research described in the article.

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