

Classification and Biological Function of ncRNAs (lncRNAs and circRNAs) in Plants

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Abstract

Non-coding RNAs (ncRNAs) are molecules that play important biological roles in plant growth but lack coding capacity. They are widely distributed in all living species. The advancement of high-throughput sequencing technology (RNA-seq) has enabled the identification of various ncRNAs. Their activities and mechanisms of action have become increasingly clear. Recent studies indicate that ncRNAs are critical for plant growth, development, and responses to environmental stress. In particular, elucidating miRNA-lncRNA-circRNA interaction processes will help identify genetic adaptations in plant stress resistance. The categorization of lncRNAs, their roles, and mechanisms in plant responses to environmental challenges are briefly summarized. The functions of ncRNAs in root and leaf development, plant growth and development, dormancy, germination, and flower formation are emphasized. Long non-coding RNAs (lncRNAs) function as sponges, precursors, scaffolds, and regulatory complexes, and serve as transcription factors (TFs) and chromatin modification structures. lncRNAs serve as regulators in epigenetics and significantly influence processes such as chromatin network remodeling and DNA methylation.

Keywords: non-coding RNA, lncRNA, circRNA, intronic, stress

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1. Introduction

It is widely accepted that biological processes in plants, including developmental physiology, biological rhythms, and stress responses, are regulated by a complex network.

The expression of protein coding genes underlies plant biological function. However, latest research has elucidated the significant functions of lncRNAs and circRNAs in plant life (Yang et al., 2023). lncRNAs have an important role in many different types of regulation, including post-transcriptional regulation, transcriptional control, and nucleus chromatin organization. These molecules are vital for controlling gene expression, which is necessary for controlling how plants adapt to their environment (Feuerstein et al., 2025). In plants, chromatin has emerged as a crucial regulator of genome design by playing a role in organization and gene expression. Plants maintain genome stability by regulating chromatin structure through DNA methylation and robust silencing of transposon elements. (Zhang et al., 2018; Bhar et al., 2023). circRNAs are a new class of ncRNAs originating from pre-mRNA by an unnatural splicing (Belousova et al., 2018). Plant circRNAs exhibit a reduced number of repetitive and reverse complementary regions in comparison to animal circRNAs. Recent studies have identified the presence of transposable mitochondrial-encoded circRNAs (mcircRNAs) in plants, alongside nuclear-encoded circRNAs (Liao et al., 2022; Bhar et al., 2023).

1.1 Classification and characteristics of ncRNA

For an extended period, the principal role of RNA was recognized as the conveyance of genetic information from DNA for protein synthesis in ribosomes by transcription (Nadhan et al., 2022). Nevertheless, the emergence of next-generation sequencing technology, along with transcriptome studies and the examination of transcriptional

noise, has underscored the functional relevance of novel non-coding RNA types (Eren et al., 2016). Most ncRNAs in plants and other animals fall into one of two main types: housekeeping ncRNAs or regulatory ncRNAs (Figure 1). There is further classification of regulatory ncRNAs based on their cellular localization and structural features. This category includes miRNAs, siRNAs, tsRNAs produced from tRNA, lncRNAs, and circRNAs, all of which are classified as non-coding RNAs (Figure 1).

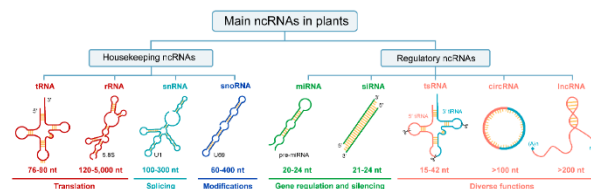


Figure 1: Classification of ncRNAs (Chao et al., 2022)

According to Chao et al. (2022), there are two primary categories of linear ncRNAs: long non-coding RNAs (lncRNAs) and short ncRNAs. Several different kinds of short non-coding RNAs are included in this category. Some examples include Piwi-interacting RNAs (piRNAs), siRNAs, and miRNAs. In most cases, lncRNAs are more abundant in cells than miRNAs. Although non-coding RNAs cannot code for proteins, they are involved in a wide variety of cellular biological processes that regulate gene expression, including epigenetic, transcriptional, and post-transcriptional pathways (Lu et al., 2024).

1.2 lncRNA

lncRNAs, a subset of non-coding RNAs, are naturally occurring RNA molecules that generally surpass 200 nucleotides in length. These entities exhibit well-defined three-dimensional structures; however, they do not have the capacity to code for proteins. The majority of these molecules are primarily found within the nucleus of eukaryotic cells (Delpu et al., 2016; Wei et al., 2017; Zhang et al., 2022; Wang et al., 2023). The functional mechanisms of nuclear lncRNAs exhibit a remarkable diversity; in particular, they engage with a range of proteins and RNA molecules to support the maintenance of nuclear architecture (Figure 2) (Nadhan et al., 2022).

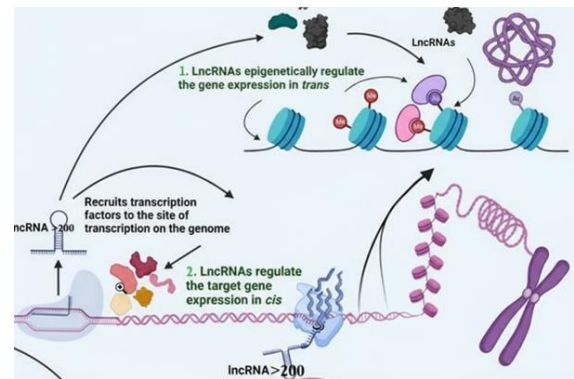


Figure 2: Interaction of lncRNAs with various proteins and RNAs (Nadhan et al., 2022)

In plants, lncRNAs are typically produced by RNA polymerase II (Pol II), although there are instances where Pol III, Pol IV, and Pol V may also be involved in this synthesis. The efficiency of splicing these transcripts is generally low (Nadhan et al., 2022). lncRNA sequences often lack an open reading frame (ORF) or are very short; therefore, they lack protein coding in the classical sense. However, some recent studies have identified rare lncRNAs that can encode short peptides in both animals and plants (Nelson et al., 2016; Zhang et al., 2022). These peptides are translated from small ORFs within the lncRNA sequence and may contribute to the regulation of certain biological processes. lncRNAs and mRNAs share some similarities in terms of their nucleotide sequence and structural features. lncRNAs transcribed by Pol II contain mRNA-specific elements such as a methylated cap at the 5' end, a poly(A) tail at the 3' end, and promoter regions. These promoter regions, in particular, mediate the regulation of gene expression by interacting with transcription factors (Lu et al., 2024).

1.2.1 Classification of lncRNAs

lncRNAs arise from various origins (Ponting et al., 2009). When assessed in relation to their positional context with protein-coding genes, they are classified into various categories. They are mainly categorized into intergenic lncRNAs, intronic lncRNAs, antisense lncRNAs, and sense lncRNAs (Figure 3) (Ma et al., 2013). Intergenic lncRNAs, commonly referred to as lincRNAs, are produced from a distinct promoter situated between two protein-coding genes (Figure 3A)

(Lu et al., 2024). On the other hand, intronic lncRNAs are derived from the intronic regions of protein-coding genes (Figure 3B) (Lu et al., 2024). Sense lncRNAs are positioned on the same strand and aligned in the same direction as protein-coding genes, as illustrated in Figure 3C. Long non-coding RNAs (lncRNAs) can include sense sequences that consist of exons from protein-coding genes, exhibit partial overlap with these genes, or even span the complete sequence of a protein-coding gene through an intron (Ma et al., 2013). Antisense lncRNAs are produced from the strand that is complementary to the strand of the protein coding gene. These regions may coincide with exonic or intronic areas, or they could extend across the full length of the protein-coding gene, including an intron (Figure 3D) (Ma et al., 2013).

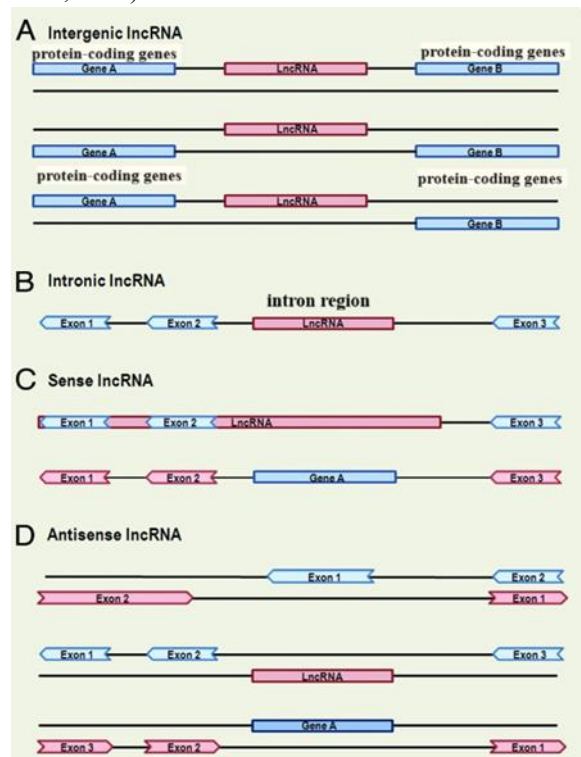


Figure 3: Classification of lncRNAs based on their relationship with protein-coding genes (Ma et al., 2013).

Plants have a low frequency of intronic lncRNAs but a high frequency of intergenic lncRNAs, which are the most functionally varied category (Traubenik et al., 2024). Many lincRNAs have expression levels that alter in response to stress

and that differ substantially among tissues. This provides more evidence that lncRNAs are involved in controlling stress responses and development and are subject to dynamic regulation. According to Wang et al. (2017), several natural antisense transcripts (NATs) have tissue-specific expression levels that can be altered by biotic or abiotic stressors.

1.2.2. The biological function of lncRNAs

lncRNAs serve as versatile regulators in plant, yeast, and animal cells. These molecules can bind miRNAs, specifically acting as sponges, thus preventing the repression of target genes. They can also act as precursors, providing precursor molecules for miRNA or siRNA production. They also play a role in nuclear architecture by interacting with transcription factors or chromatin modification enzymes, forming scaffolds or regulatory complexes. They also act as stabilizers, increasing the half-life of mRNAs. As epigenetic regulators, they can influence processes such as chromatin remodeling or DNA methylation. Furthermore, lncRNAs can regulate gene expression through either cis or trans effects, altering the activity of the promoter closest to the gene or regulating the expression of distant genes. Consequently, lncRNAs are important components of the regulatory network in plant processes such as growth, development, signal transduction, and stress response (Zhang et al., 2023; Lu et al., 2024).

1.3 circRNA

Circular RNAs (circular RNA) are widely distributed in living organisms. They are characterized by a distinct closed-loop structure and are single-stranded, endogenous non-coding RNA molecules (Figure 4). These molecules are formed by back-splicing of pre-mRNAs. Their length varies depending on the number and length of exons or introns of the gene from which they originate (Chao et al., 2022). Sanger et al. (1976) initially defined circRNA as a "single-stranded, covalently closed, circular RNA molecule." Many species exhibit the non-natural process of back splicing, which is responsible for the production of circRNAs. This process entails the covalent joining of the 5' and 3' ends. circRNAs are less likely to be degraded by RNase R and have

greater stability than linear RNAs because of their closed-loop structure (Yadav et al., 2024).

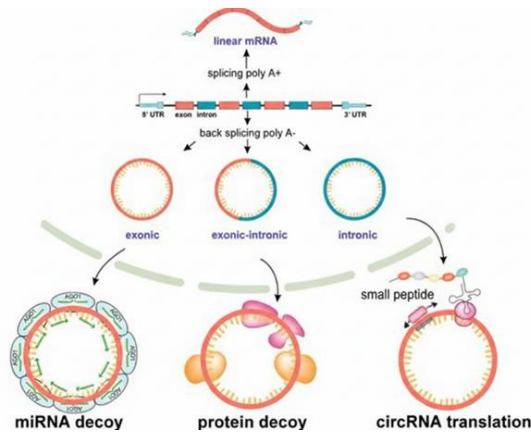


Figure 4: Regions and composition of circRNA sources (Chao et al., 2022)

Although studies on circRNAs in plants have only recently begun, the biological functions of these molecules are increasingly being elucidated. circRNAs are classified into four main groups based on their regions of origin (Lu et al., 2024). They are grouped as exonic circular RNA (ecircRNA) (Figure 4), intronic circular RNA (ciRNA) (Figure 4), mixed exon–intron circular RNA (eIciRNA) (Figure 4), and intergenic circular RNA (intergenic circRNA). These molecules are formed by the reverse splicing of the 5' splice donor site and the 3' splice acceptor site. Therefore, they are synthesized by back-splicing (Zhang and Dai, 2022). While normal splicing involves the removal of an intron and the joining of two adjacent exons, in back-splicing, the downstream splice donor site combines with the upstream splice acceptor site to form a circular structure. In the early stages of circRNA discovery, they were overlooked due to their low abundance in the cell. However, subsequent molecular analyses have shown that circRNAs possess high stability (Lu et al., 2024). Unlike linear RNAs, these molecules lack a 5' methyl cap and 3' poly-A structure; therefore, they are not easily degraded by RNase enzymes. This gives circRNAs their long half-life and structural stability (Zhou et al., 2022). circRNAs also stand out for their high sequence conservation, tissue- and developmental stage-specific expression, and rich diversity.

1.3.1. The biological function of circRNAs

CircRNAs have played versatile biological roles in many living organisms, including plants and other organisms. These roles include functional functions such as interaction with miRNA, RNA-binding proteins (RBPs), polypeptide coding potential, and transcriptional regulation. CircRNAs can interact with miRNAs and act as competitive endogenous RNAs (ceRNAs). In this case, the circRNA binds a specific miRNA like a sponge, negatively regulating its activity and its repressive effect on the target gene. CircRNAs interact directly with RBPs, regulating processes such as RNA processing, splicing, and folding. Furthermore, circRNAs generally do not encode proteins; however, in recent years, it has been observed that some circRNAs have the ability to encode polypeptides or small peptides. These small peptides can regulate the expression of related genes or metabolic processes (Song et al., 2023). In their role in transcriptional regulation, some nuclear-localized circRNAs can directly affect gene transcription. For example, they can increase or repress gene expression by interacting with promoter regions in DNA or transcription factors. The multifaceted roles of circRNAs described above indicate that they are not merely byproducts of RNA activity; rather, they are active regulatory molecules in fundamental biological processes such as gene expression, signal transduction, and stress responses (Lu et al., 2024).

1.4 The roles of ncRNAs in seed dormancy, germination, and seedling development

Seed dormancy and germination processes are determined by both environmental factors and genetic mechanisms. ncRNAs serve as intracellular molecular regulators in this process. They play an active role in biological stages such as seed maturation, dormancy, emergence, and root elongation (Tognacca and Botto, 2021). In studies on lncRNAs, it was observed that the lncRNA HID1 in *Arabidopsis* reduced ABA synthesis by repressing the NCED9 gene, the rate-limiting enzyme in ABA biosynthesis, thereby preventing seed dormancy (Wang et al., 2023). In cabbage (*Brassica oleracea*), the lncRNA BoNR8 was found to affect germination by regulating ABA signaling genes (Wu et al., 2019). The lncRNA AtR8 has been reported to regulate seed

germination under salt stress conditions (Zhang Nan et al., 2020). Studies with circRNAs have shown that while the germination rate of Os06circ02797 mutants in rice remains unchanged under normal conditions, it decreases significantly under salt stress. This molecule binds OsMIR408 like a sponge, altering the expression of relevant target genes. Thus, it is known to control germination and other developmental processes by establishing a circRNA-miRNA-mRNA regulatory network (Zhou et al., 2021).

1.5 The roles of ncRNAs in the development of the plant's vegetative organs (roots, leaves, etc.)

ncRNAs (lncRNAs and circRNAs) regulate the development of vegetative organs such as roots, stems, and leaves in plants through layered and complex network pathways. In a 2019 study, Liu et al. identified 695 different lncRNAs in *Arabidopsis* roots, and observed that T5120, in particular, promoted root development by enhancing the nitrate response. Similarly, in *Arabidopsis*, an antisense lncRNA called MAS was found to control flowering time at low temperatures by regulating the transcription of the MAF4 (FLOWERING4) gene (Zhao et al., 2018). A study in rice indicated that the TWISTED LEAF (TL) antisense lncRNA regulated OsMYB60 expression and leaf morphology (Liu et al., 2018). MSTRG.16920 and MSTRG.7613 lncRNAs were observed to delay leaf senescence in *Solanum lycopersicum* by repressing target NAC transcription factors during senescence (Li et al., 2022). In circRNA studies, it was observed that overexpression of laciRNA from the At5g37720 gene in *Arabidopsis* caused phenotypic changes such as leaf curling, flowering time, and fertility (Cheng et al., 2018).

According to Swiezewski et al. (2009), the *Arabidopsis* flowering locus (FLC) seems to be a floral repressor that inhibits the expression of genes that promote flowering, therefore preventing premature blooming. This is based on our examination of the involvement of lncRNAs in the chromatin conformation structures of FLC. The 3'-end FLC promoter is responsible for the production of the non-coding RNA COOLAIR, a key regulator of FLC. COOLAIR has the ability to produce different isoforms by means of polyadenylation at the 3' end. This process

differentiates between Class II transcripts, which are 600-750 nt in length, and short Class I transcripts, which are around 400 nt in length, as a result of alternative splicing of certain exons (Hawkes et al., 2016). It has been found that some COOLAIR isoforms contribute to the quick blooming of warm-grown plants and to the silencing of chromatin through the development of R-loops.

Abiotic stressors, such as FLC transcriptional suppression, activate a network of molecules at the FLC locus that regulate FLC transcription. Consequently, COOLAIR may increase blooming in response to all temperatures by directly regulating FLC levels (Hawkes et al., 2016; Prall and Gregory, 2022).

The RNA-binding protein FCA connects with the CURLYLEAF (CLF) component of the Polycomb Repressive Complex 2 (PRC2) after interacting directly with COOLAIR. It has a role in chromatin loop creation and remodeling. An active chromatin loop is composed in the space between the promoter and the 3' end of the gene in plants that have not undergone vernalization. This arrangement allows: for a high level of FLC expression. Additionally, at the FLC-COOLAIR locus, COLDAIR and COLDWRAP interact with PRC2 to pave the way for the formation of a restrictive intragenic chromatin loop that links the FLC promoter to the first intron (figure 5). This loop is activated by vernalization. According to Feuerstein et al. (2025), this interaction helps stabilize gene silencing and increases the propagation of H3K27me3.

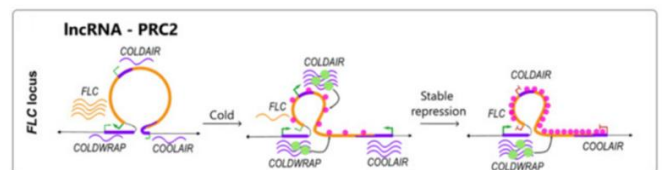


Figure 5: Interaction of lncRNA with COLDAIR and COLDWRAP during vernalization (Feuerstein et al., 2025).

The expression of the overlapping coding gene VRN1 is directly regulated by the long non-coding RNA VAS in wheat. To speed up the vernalization-mediated blooming process in winter wheat, the alternatively spliced lncRNA VAS is crucial for activating Vernalization 1

(VRN1). In the early stages of vernalization, the MADS-box transcription factor TaVRN1 is active (Trevaskis, 2010). Similar to TaVRN1, VAS is an alternate non-coding transcript of 662 nucleotides that begins transcription at the same position. This long non-coding RNA forms a physical association with RF2b, a bZIP transcription factor recognized for its role in promoting the expression of TaVRN1 and hastening flowering in reaction to vernalization. Operating within a complex formed by lncRNA and transcription factors, VAS interferes with the chromatin loop at the TaVRN1 locus, which facilitates the binding of the transcription factor to regulatory regions (Figure 6). As a result, the cold-induced lncRNA VAS brings together the transcription factor RF2b to facilitate gene expression (Xu et al., 2021; Feuerstein et al., 2025).

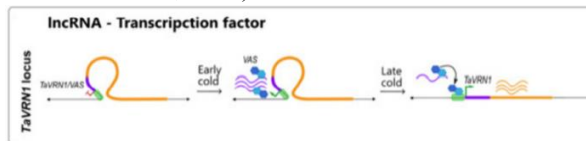


Figure 6: VAS (lncRNA-Transcription factor) in wheat (Feuerstein et al. 2025).

2. The Role of lncRNAs and circRNAs in Stress Responses in Plants

Stressors in the environment can have a direct impact on plants. Their physiological, biochemical, and molecular reactions to these stressors are intricate and multifaceted. Signal transduction, signal perception, gene expression control, stress-related protein synthesis, cell membrane remodeling, metabolic adaptation, and abiotic and biotic stress response mechanisms are among the many that plants have evolved (Lu et al., 2024). Novel ncRNAs play an essential role in these stress networks, according to recent research. Researchers have shown that non-coding RNAs (ncRNAs) can increase plant tolerance and adaptive capacity by regulating the expression of target genes in response to stress. This, in turn, changes the efficiency of metabolic pathways and signaling systems.

2.1 The Role of ncRNAs in Abiotic Stress Responses

Abiotic stress does not pose a direct biological threat to living organisms; it does so by disrupting their physiological functions and severely affecting growth

and yield. Recent studies have shown that numerous miRNAs, circRNAs, and lncRNAs play regulatory roles in plant responses to abiotic stresses (Zhang et al., 2019b, 2021; Xia et al., 2023). A study in *Cucumis sativus* (Zhu et al., 2019) showed that circRNAs increased stress tolerance under salt stress by regulating the expression of genes related to transcription, cell cycle, and proline metabolism (Lu et al., 2024). In *Glycine max*, 749 circRNAs were identified under low-temperature conditions, and bioinformatic analyses revealed that they responded to low-temperature stress via circRNA–miRNA–mRNA networks (Wang et al., 2020). As for lncRNAs, in *Arabidopsis thaliana*, the lncRNA DRIR, while its expression level is normally low, was observed to increase significantly under drought, salt stress, and ABA treatment. Overexpression of DRIR has been found to increase plant resistance to these stresses (Qin et al., 2017; Lu et al., 2024). Studies in rice have shown that after short-term drought, some lncRNAs activate photosynthesis and proline biosynthesis pathways, creating a “drought memory” (Li et al., 2019). In a study in *Betula platyphylla*, the lncRNA LncY1 was observed to increase resistance to salt stress by regulating the transcription factors BpMYB96 and BpCDF3 (Jia et al., 2023).

2.2. The Role of ncRNAs in Biotic Stress Responses

Plants are exposed to biotic stresses induced by pathogens (bacteria, fungi, viruses) and pests (insects, nematodes) throughout their growth processes. These stresses lead to serious yield losses in agriculture. Studies have demonstrated that circRNAs and lncRNAs play a key role in defense responses to biotic stresses (Lu et al., 2024). In *Oryza sativa*, an increase in circRNA diversity was observed following *Magnaporthe oryzae* (rice blight) infection. In particular, circR5g05160 was highly expressed in disease-resistant lines and enhanced disease defense (Fan et al., 2020). In maize (*Zea mays*), more than 30 circRNAs were identified following maize Iranian mosaic virus (MIMV) infection, and some of these circRNAs interacted with miRNAs to regulate metabolic and defense pathways (Ghorbani et al., 2018). Zhang et al. (2022) conducted a study on cotton, in which lncRNA2 and lncRNA7 were found to contribute to *Verticillium pathogenicity* resistance by regulating genes associated with cell wall defense. In particular, the small peptide encoded by lncRNA7

strengthened resistance by increasing the expression of PSK- α , ARF5, and GbPMEI13, while lncRNA2 had the opposite effect by activating GbPG12. The findings clearly demonstrate the direct role of lncRNAs and circRNAs in the complex RNA regulatory networks that plants develop to respond to biotic and abiotic stresses.

3. Conclusion

Numerous plant biological activities rely on non-coding RNAs (ncRNAs), such as development, growth, reproduction, metabolic control, and responses to both biotic and abiotic stress. Much progress has been achieved in comprehending the variety, expression patterns, and regulatory mechanisms of ncRNAs as a result of the fast evolution of transcriptome and high-throughput sequencing technology. The intricate regulatory network that coordinates gene expression at the epigenetic, transcriptional, and post-transcriptional levels is now understood to be mostly composed of ncRNAs and their interactions with one another. Discovering the molecular basis of plant stress resistance requires investigating miRNA-lncRNA-circRNA interactions in ncRNA networks, especially in the context of drought, salinity, and pathogen stress, and thoroughly clarifying the processes involved in stress tolerance. Researchers have discovered that long non-coding RNAs (lncRNAs) and circular RNAs (circRNAs) play a crucial role in plant tolerance to both biotic and abiotic stress factors throughout their entire life cycle. Bioinformatics, agricultural biotechnology, and multi-purpose research on ncRNA plant biology will one day provide biomarkers and biosensors, laying the groundwork for sustainable agriculture, improved product quality, and plant breeding.

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