
EXPERIMENTAL PAPERS

Regulatory Non-Coding RNAs in Crops Health and Disease

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Abstract—For many years it was thought that the function of RNA was limited to the process of producing proteins. In recent years, scientific discoveries have been proving the multiple roles of different RNAs in different regulatory mechanisms. These RNA's are collectively called non-coding RNA's (ncRNA's). This review presents the latest advances on the different classes of non-coding RNA's (ncRNA's) from their function to mechanisms of action. Special emphasis is given to the long non-coding RNAs as new regulatory elements in eukaryote gene expression and in the processes of epigenetic regulation in plants. We believe that increasing studies of regulatory non-coding RNAs in plants will provide a better understanding of the different types of genes related to crop resistance.

Keywords: ncRNAs, miRNAs, lncRNA

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CENTRAL DOGMA OF MOLECULAR BIOLOGY

Genes are nucleotide segments responsible for containing the information necessary for the synthesis of biologically active and functional products such as [1] for example proteins. The importance of understanding the functioning of the different types of representative genomes of each species, led to the emergence of a new science, genomics. According to the National Human Genome Research Institute, genomics is defined as the study of all the genes of a species (its genome), including their gene interactions and interactions with the environment.

The central dogma of molecular biology indicates that a DNA molecule is transcribed into an RNA molecule, which in turn is translated into a protein [2]. Protein synthesis has two phases: (I) transcription; and (II) translation. In transcription, the DNA molecule is opened by breaking the hydrogen bonds that unite the nucleotides to allow the enzyme RNA polymerase to copy the information and synthesize the messenger RNA (mRNA) in the 5' to 3' direction. It is also important to mention that it is during the transcription phase that a very important process called splicing occurs, in which the pre-mRNA can undergo some modifications, namely with the removal of introns but also, in some cases, of exons.

After transcription, translation begins, this process takes place in the cytoplasm, more precisely in the ribosomes. There, the codons of the mRNA are paired with their corresponding anticodons of a molecule of transfer RNA (tRNA), which carries the amino acids. Each codon represents a three-nucleotide sequence that depicts a single amino acid of the genetic code, or a termination signal. Protein translation always starts with the initiation codon (AUG) and ends with one of the stop codons (UAG, UAA, or UGA). The result of this whole process is the formation of a protein [3, 4].

In 1970, when the central dogma of molecular biology was first presented, researchers thought that the only function of RNA's was to ensure the production of proteins from DNA. They were convinced that RNA's had no other function besides this process. However, in recent years, new scientific discoveries have proven that there is a variety of non-coding RNA molecules capable of performing several important roles in the cellular structure as a whole [5–8]. Next, we will present some of the functions of non-coding RNAs.

CLASSES OF ncRNAs

The transcriptome is the set of RNA cells expressed in a particular tissue [9]. According to some authors [10–12], above than 90% of the human genome is transcribed, but, only about 2% represent protein-coding genes (Fig. 1). This indicates that most tran-

Table 1. Small ncRNAs are classified according to their possible functions within the cell [20–25]

Name	Meaning	Function
miRNA	MicroRNA	Putative translational regulatory gene family
siRNA	Small interfering RNA	Active molecules in RNA interference
endo-siRNA	Endogenous small interfering RNAs	Acts as post-transcriptional regulator that target RNAs
snRNA	Small nuclear RNA	Includes spliceosomal RNAs
snoRNA	Small nucleolar RNA	Most known snoRNAs are involved in rRNA modification
stRNA	Small temporal RNA	Interrupt the translation of mRNAs
piRNA	Piwi-interacting RNAs	Acta in the regulation of translation and mRNA stabilization
ra-siRNA	Small interfering RNA	Acts in the silencing of gene transcription through chromatin
vtRNA	vault RNA	Located at a conserved genomic locus linked to the protocadherin gene cluster
Y RNA	Y RNA	Associated with chromosomal DNA replication

scribed genes create non-functional RNAs (ncRNAs), whose functions are characterized especially as maintenance or non-regulatory RNAs [10–12], whose encodings are different in cellular metabolism [13].

In addition, ncRNAs have demonstrated important functions in cell structure, as well as in catalytic and regulatory processes in the cell [14], such as regulation of gene expression [15, 16], regulation of protein synthesis or of other nucleic acids, including DNA and other types of RNA [17–19].

Another important feature of ncRNAs is that the fact that another protein is not produced from a transcript is not a sufficient requirement to characterize an ncRNA, because in some, this transcript may end up being translated once exposed to environmental or physical conditions [5, 20]. This is one of the main problems encountered by computational methods to classify RNAs.

NcRNAs are divided into two subclasses: NcRNAs called *small or short non-coding RNAs* such as miRNAs, siRNAs, snRNAs, endo-siRNAs, snoRNAs, stRNAs, piRNAs, rasiRNAs, vtRNAs, Y RNAs (Table 1) [21–26] and long non-coding RNAs (lncRNAs) which include the Xist, Evf, Ar, CTN and PINK [27–30]. The miRNAs, belonging to a subclass of short non-coding RNAs, have become quite notable in research, mainly because they play important roles in the regulation of various cellular processes, being in some cases used as potential treatment targets or biomarkers [31, 32]. RNA polymerase II is responsible for transcribing miRNAs. The miRNAs are endogenous molecules of ribonucleic acid (RNA), non-coding, with about 22 nucleotides (nt), act as regulators of gene expression in plants and animals, at the post-transcriptional level through the cleavage of a messenger RNA (mRNA) target or translation repres-

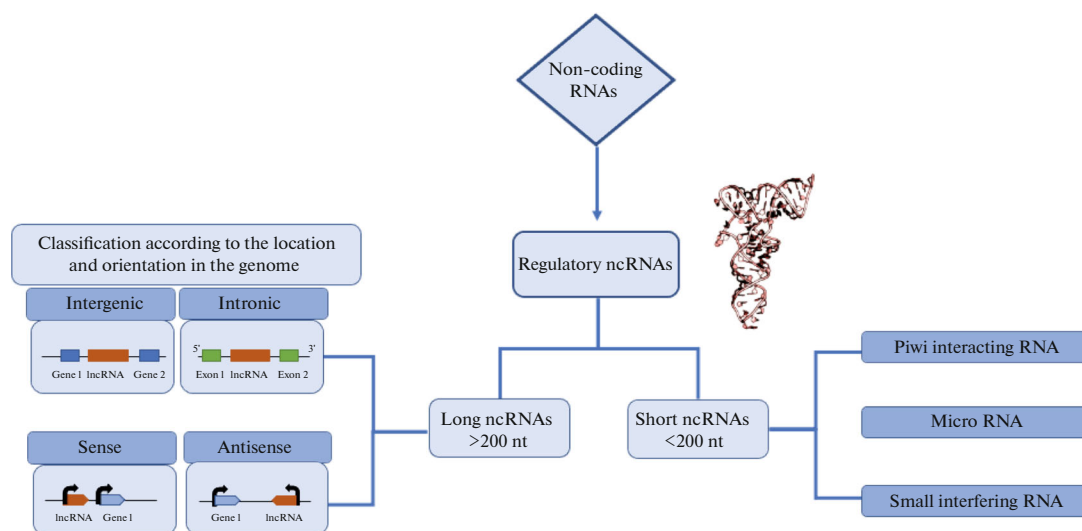


Fig. 1. Classification of noncoding of noncoding RNAs. The scheme presents the classification of noncoding RNAs according to their function, size, and location in the genome. Adapted from [14].

sion. Their main function is to act as post-transcriptional silencers, as they pair with specific mRNAs and regulate their stability and translation. Each miRNA can have hundreds or thousands of targets, and an mRNA can be inhibited by different miRNAs. Plant miRNAs are a near perfect match to their mRNA targets and induce gene repression through cleavage of target transcripts [33, 34].

MECHANISM OF ACTION OF miRNAs

The functional miRNA is related to the Argonaute 2 (Ago2) protein as it is part of the RNA-induced silencing complex (RISC). The miRNA directs the RISC complex to interact with the target mRNA, aided by the complementarity between the miRNA seed sequence (nt 2–7) and the target mRNA sequences that are usually located at the 3' UTR end [35]. However, these sequences can also be found at the 5' UTR end and in the coding sequence itself. The interaction between the miRNA and its target mRNA in the RISC complex causes the silencing of mRNA expression through two possible mechanisms: (I) If the complementarity between the miRNA and the mRNA is perfect, Ago2 endonucleolytically cuts the mRNA, causing its degradation directly; (II) If the complementarity is imperfect, as is most often found in animal cells, the mRNA is translationally repressed through its destabilization by shortening the polyA at the 3' end and the loss of its 5' cap structure [36]. According to the authors O'Connell et al. [37], the synthesis of target mRNA proteins is repressed between 1.2 and 4 times, so that miRNAs are designated as fine regulators of gene expression. Furthermore, the same miRNA can have several target mRNAs and vice versa, i.e., the same mRNA can be regulated through several miRNAs [38], which normally belong to the same family of miRNAs, creating networks complex regulatory processes through which combinations of miRNAs with mRNAs can occur. According to the authors Ala et al. [39], the complexity of the regulatory network mediated by miRNAs increases considerably if we add the fact that miRNAs can be "stealed" by endogenous competing RNAs (ceRNAs) to prevent their function repressive.

LONG NON-CODING RNAs AS NEW REGULATORY ELEMENTS IN EUKARYOTE GENE EXPRESSION

One of the major changes caused by NGS (Next Generation Sequencing) was the fact that it allowed to obtain a huge volume of data at relatively low prices, when compared to those initially practiced [40, 41]. Developments in sequencing techniques have shown that, contrary to what was supposed, most eukaryotic genomes are transcriptionally active [41].

Thanks to advances in sequencing platforms, it was possible to identify numerous non-coding transcripts (ncRNAs) with numerous biological functions hith-

erto unknown [42, 43]. In general, lncRNAs can be found both in the nucleus and in the cytoplasm and their levels are lower than those of protein-coding RNAs, moreover, their expression is usually tissue-specific [44, 45]. According to some authors [46, 47], lncRNAs are less conserved at the sequence level than mRNAs, however, at the level of their secondary structures, they appear to be highly conserved. Thanks to the new sequencing technologies mentioned above, it was also possible to build a database of Long non-coding RNA in plants (PLncDB V2.0), using more than 1246372 lncRNAs from 80 plant species [48].

lncRNAs are usually catalogued based on the location they occupy in relation to nearby annotated genes. Thanks to this, it is possible to distinguish between lncRNAs located in intergenic regions (intergenic lncRNAs) and lncRNAs that are overlapping with the sequence of a nearby gene [49, 50] (Fig. 1). Still regarding lncRNAs that overlap with the sequence of a nearby gene, these may be located totally or partially within an intron (intronic lncRNAs) or in some cases, directly overlapping with the sequence of an exon. However, if the lncRNA is transcribed in the same direction as the gene it is identified as sense lncRNA, and if it is in the opposite direction, it is identified as natural antisense lncRNA (NAT-AS) [51, 52]. In some situations, the position of lncRNA in the genome is closely related to the function it performs [51, 52].

LONG NON-CODING RNAs IN PLANTS

Plants do not have the ability to move around like other living beings, however, they have developed numerous molecular mechanisms that help them adapt to the most varied stresses to which they are constantly subjected. The stresses caused to plants are mainly due to attacks by pathogens, but also to environmental stresses such as drought and high and low temperatures [53].

In recent years, several groups of researchers [54–61] have carried out transcriptomic analyzes in more than 38 plant species with the objective of identifying lncRNAs, as was the case of *Zea mays*, *Oryza sativa*, *Solanum lycopersicum*, *Solanum tuberosum*, *Glycine max*, *Medicago truncatula* or *Arabidopsis thaliana*. Unlike mRNAs, lncRNAs do not have the ability to encode proteins of their own, they usually act as structural, catalytic, or regulatory molecules [62].

Some studies carried out [63–72] showed that lncRNAs were associated with essential biological processes, such as the protection of genome integrity, transport of auxins, response to pathogen attacks, alternative splicing, photomorphogenesis, phosphate homeostasis, response to abiotic stress situations or in flowering. In Table 1 we can see a list of long non-coding RNAs (lncRNAs) identified in plants under fungal pathogen stress.

lncRNAs can also interact with miRNAs, according to the authors [73], sometimes the lncRNA can be

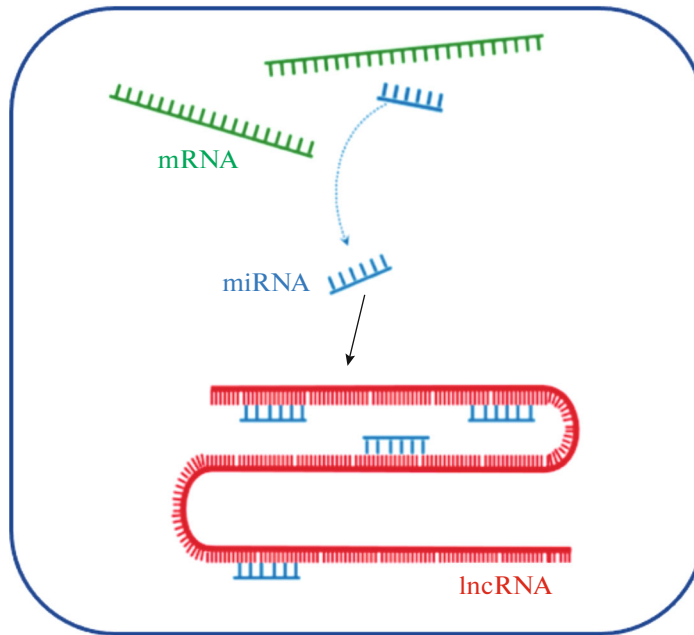


Fig. 2. IncRNAs used to “attract” the miRNA and pair with it, thereby preventing interaction between the miRNA and its target genes allowing regulation of miRNA target gene function. Adapted from [53].

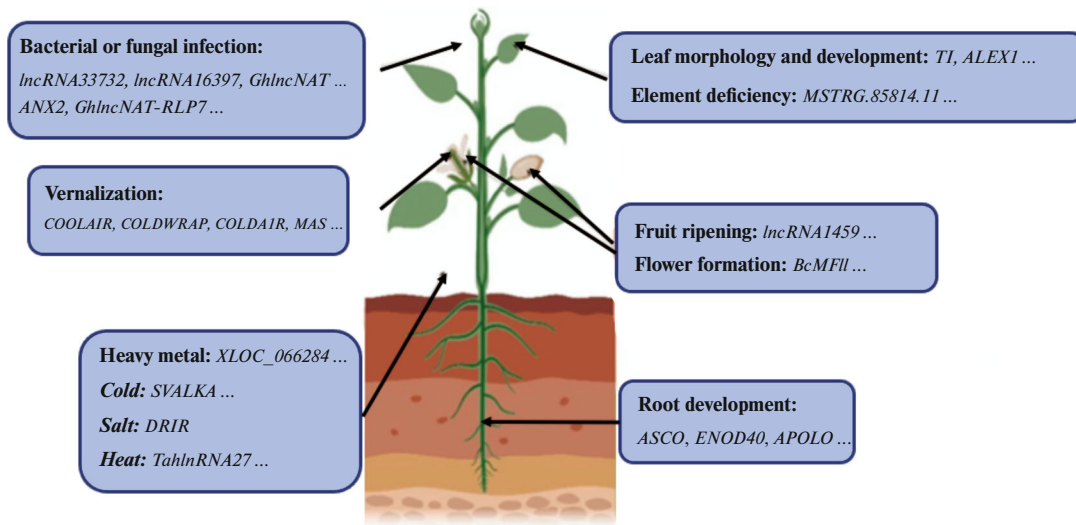


Fig. 3. Some functions of various IncRNAs in plant. Adapted from [53].

used to “attract” the miRNA and pair with it, thus preventing the interaction between the miRNA and its downstream target genes, allowing the regulation of the target gene function. of the miRNA (Fig. 2).

TRANSCRIPTIONAL REGULATORY PROCESSES MEDIATED BY IncRNAs IN PLANTS

In 2018, Kindgren and his collaborators [67] carried out a study that allowed the analysis of an

IncRNA implicated in the control of the acclimatization process of the *Arabidopsis* species at low temperatures, this antisense IncRNA was called SVK. SVK receives the designation of antisense because its expression is induced after that of the CBF1 gene and interrupts its transcription. Kindgren and colleagues [67] proposed that CBF1 expression is being downregulated by SVK, thanks to a co-transcriptional collision process of RNA polymerase II.

According to the authors Seo et al. [69], a IncRNA designated by ELENA1 is implicated in the activation

of the Arabidopsis immune response. That is, according to the same authors, the expression of this lncRNA is induced by the presence of *elf18* and *flg22* response elicitors to pathogens, which interact with the 19a subunit of the mediator complex. This interaction that occurs between *elf18* and *flg22* with the 19a subunit is extremely important to be able to direct the mediator complex to the promoter region of the *PR1* gene. The *PR1* gene is responsible for encoding a protein that aids in the immune response [69].

EPIGENETIC REGULATORY PROCESSES MEDIATED BY lncRNAs IN PLANTS

Some authors [74, 75] have described and characterized the function of several lncRNAs (Fig. 3), functions such as, namely, participating in the control of gene expression at the epigenetic level. According to Nejat and Mantri 2017 and Tian et al. [75, 76], the lncRNAs *COLDWRAP*, *COOLAIR* and *COLDAIR* are associated with the vernalization process of some plants, a process that allows plants to transition to the reproduction phase after being exposed to a long period of cold (however, not all plants have this ability to carry out the vernalization process). The lncRNAs collaborate in the transcriptional repression of the *FLC* gene, this gene was identified as being an inhibitor of floral transition throughout the vernalization process [77–79].

Another lncRNA involved in the epigenetic control of some plants, namely in gene expression is *APOLO*. *APOLO* is a lncRNA transcribed by polymerases II and V and is normally located in the promoter region of the *PID* gene, which is responsible for regulating auxin transport in Arabidopsis [65, 80]. The expression of *PID* and *APOLO* is activated by auxins [65]. That is, *APOLO* interacts with the *LHP1* protein taking it to the *PID* promoter region [65]. In this region, the interaction of *LHP1* with chromatin promotes the formation of a loop, which is responsible for the decrease in the expression of *PID* and *APOLO* itself, enabling the correct development of the root [65].

lncRNA33 732 and *lncRNA16397* respond to infections caused by pathogens [81, 82]. *GhIncNAT-ANX2* and *GhIncNAT-RLP7* are a pair of lncRNAs that act in the regulation of pathogenic infection but are also associated with increased disease resistance in cotton [83]. *lncRNA1459* play a role in the fruit ripening process [84]. *ASCO* alters root development [85]. *enod40* acts in the formation of root nodules [86]. *MSTRG.85814.11* intervenes in the response caused by iron deficiency [87]. *XLOC 086307*, *XLOC 086119* and *XLOC 066284* act in response to the heavy metal cadmium [88].

CONCLUDING REMARKS

The area of investigation of ncRNAs has undergone rapid and important changes over the last few

years, demonstrating the importance that these nucleic acids have in cell biology, thus contradicting what was initially thought. It is expected that this new field of knowledge will enable the development of new drugs that will be used in personalized medicine for the human being. However, it is important to mention that further studies are needed, namely in terms of pharmacokinetics or their use in terms of biomarkers, as for example in the case of miRNAs in which they are used as circulating biomarkers in body fluids.

Regarding the use of nRNAs in plants, these have been used in the treatment of several phytopathologies, helping the development of several techniques associated with a considerable improvement in the agricultural sector. Unlike the animal kingdom, plants obey systemic signals, signals that come from the sites of infection and whose function is to trigger innate immunity through resistance genes (R). However, these genes are often overtaken by the existence of epidemic pathogens. In this sense, knowing better the mechanisms of resistance can be fundamental in the control of numerous diseases and in the reduction of crop losses. Plant resistance mechanisms involve thousands of genes, including lncRNAs. Characterization of the function of lncRNAs in plants remains quite limited and one of the reasons is the lack of sequence similarity of homologous lncRNAs in cultures.

We believe that increasing studies of regulatory non-coding RNAs in plants will provide a better understanding of different types of genes related to crop resistance. Furthermore, a better understanding of ncRNAs may be beneficial for the development of new tools that use resistance genes for the biotechnological improvement of crops.

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DATA AVAILABILITY

All data generated or analyzed during this study are included in this published article (and its supplementary information files).

ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This work does not contain any studies involving human and animal subjects.

CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

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