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The functions of long noncoding RNAs in plants

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Noncoding RNAs are emerging as major regulators in plant development and environmental response. MicroRNAs, small RNAs, and ribosomal RNAs have established mechanisms for generation, maturation, and function. However, long noncoding RNAs (lncRNAs) currently lack a robust classification according to their function. lncRNAs are here defined as noncoding RNAs that are longer than 200 nucleotides and generally transcribed by RNA polymerase II. They often exhibit low expression and limited sequence conservation yet display tissue or stress-specific regulation. Furthermore, lncRNAs are categorized based on their location relative to nearby genes, including sense (overlapping a gene on the same strand), antisense (overlapping on the opposite strand), intronic (located within intron), intergenic (found between genes), and bidirectional (transcribed in the opposite direction from a nearby gene). Here, we summarized the last years of work in the field of lncRNA, but instead of grouping them into the biological processes they are involved in, we attempt to group them into general functions in plants. This will not be an exhaustive grouping of known functions for lncRNA, rather a list of established functions with several characterized cases.

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The functions of long noncoding RNAs

Tremendous effort has been put into identifying long noncoding RNAs (lncRNAs) over the years. However, described functional molecular mechanisms are few and often idiosyncratic and it has been challenging to envision general roles, if any, for lncRNAs in plants. There is also an understandable weight on studies from *Arabidopsis thaliana* (Arabidopsis), making plant-specific mechanisms difficult to predict, yet we are now reaching a critical mass of studies, and by comparing them to known mechanisms in other eukaryotes, we can now start to pinpoint some common functions described in the following.

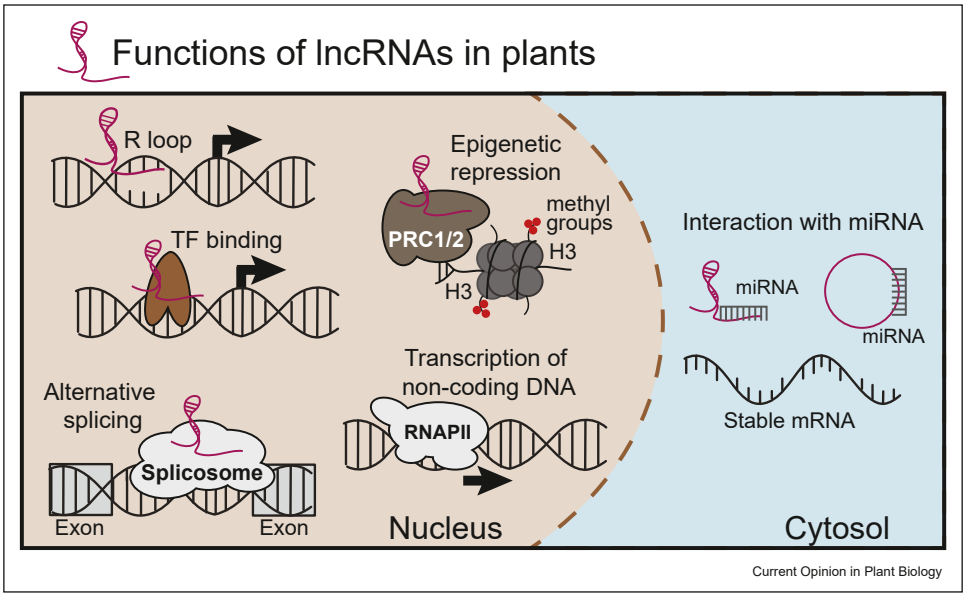
Repression by Polycomb Repressive Complex

It has been established in eukaryotes that lncRNAs function as molecular scaffolds, guides, or decoys, refining the expression of target genes through interactions with chromatin-modifying complexes, such as Polycomb Repressive Complex 1 and 2 (PRC1 and PRC2) [1,2]. The interaction of an lncRNA with PRC2 was first described in plants for *COLDAIR*, which recruits PRC2 to silence *FLOWERING LOCUS C* during the vernalization process [3]. Since then, several lncRNAs have been documented to lead PRC2 to chromatin, catalyzing the repressive trimethylation of histone H3 at lysine 27 (H3K27me3). lncRNAs orchestrate this process by directing PRC2 to specific genomic loci, thus initiating chromatin compaction. For an lncRNA to effectively recruit PRC2, it typically originates in *cis*, contains a defined motif or domain for PRC2 binding, remains nuclear, and is sufficiently stable [4] (Figure 1).

Recent studies have unveiled many lncRNAs in Arabidopsis that interact with PRC2. For instance, *SVALKA* regulates the cold response by recruiting PRC2 to deposit H3K27me3 on *CBF3* [5]. Additionally, *AG-incRNA4*, which is transcribed from the second intron of the *AGAMOUS* gene (*AG*), *represses AG* expression in vegetative tissues [6]. Another relevant case is the antisense intragenic lncRNA *SEAIRa*, which is produced from the 3′ end of *SERRATE*. The cleavage of *SEAIRa*, leads to an accumulation of H3K27me3 at the first exon of *SERRATE*, albeit it is unclear if *SEIRa* directly interacts with PRC [7]. In another example, *SABC1* acts as a molecular switch between plants defense and growth by modulating *NAC3* transcription [8]. Moreover, in response to abscisic acid and auxin, the lncRNAs *MARS* and *APOLO*, respectively, interact and titrate the PRC1 interacting protein LIKE HETEROCHROMATIN PROTEIN 1 (LHP1) away to decrease H3K27me3 at target loci [9,10].

Current research is actively revealing more lncRNAs that contribute to chromatin modification pathways that go beyond H3K27me3, highlighting the complex and layered nature of epigenetic regulation. Both histone

Figure 1



Established functions for lncRNAs in plants. lncRNAs in plants can be classified according to their function. Direct transcription regulation is accomplished through R-loops and TF binding. Indirect regulation of transcription can be the result of PRC1/2 interaction and transcription of noncoding DNA sequences (in this case, the lncRNA is unstable and not part of the regulation). Via spliceosome interaction, lncRNAs can dictate the fate of mRNA isoforms. In the cytosol, lncRNAs function as miRNA sponges to relieve mRNA cleavage. All mentioned functions are crucial for the plant's response to environmental stress and development. lncRNA, long noncoding RNA; TF, transcription factor; miRNA, microRNA; PRC, Polycomb Repressive Complex; mRNA, messenger RNA.

acetylation and H3K4me3 have been implicated as regulated by lncRNAs [11–13]. For PRC, the PRC1 component LHP1 and PRC2 component CURLY LEAF (CLF) seem especially favored as a target for lncRNAs. An outstanding question for these lncRNAs is how they convey specificity and how they are recognized by their protein partners (motif, secondary structure, etc.) to enable robust prediction of novel lncRNAs with this function.

Regulation of mRNA transcription

lncRNAs play a crucial role in the regulation of messenger RNA (mRNA) transcription by directly interacting with the transcriptional machinery and modifying chromatin architecture. This includes key regulatory processes like R-loop formation and transcription factor modulation (Figure 1).

R-loops are a common feature in eukaryotic genomes. In plants, they are especially prevalent in promoter regions [14] and their formation has been found to be responding to the environment [15]. R-loops involve the interaction of RNA with complementary DNA sequences to create DNA:RNA hybrids. These structural modifications can affect RNA polymerase II activity and the accessibility of chromatin. The Arabidopsis lncRNA *CAS/SVK* shows induction to cold stress, which leads to intergenic R-loops at *CBF* locus. These R-loops decrease nucleosome density, which leads to increased chromatin accessibility and transcriptional activity [16]. Another lncRNA, *APOLO*, creates R-loops at regions that respond to auxin, which affects both chromatin loop organization and promoter accessibility [17].

Antisense lncRNAs are transcribed from the opposite strand of overlapping protein-coding genes. For example, lncRNA *nalncFL7* in rice functions as a natural antisense transcript that originates from the opposite strand of *FL7* to regulate MAPK signaling. The RNA-binding protein BPL3 stabilizes *nalncFL7* while blocking *FL7* transcription elongation [18].

lncRNAs can directly control transcription factors by influencing their localization and availability. For instance, the lncRNA *ALEX1* in rice binds to ARF3, a transcription factor, changing its structure in the nucleus. This interaction helps ARF3 to form active dimers that repress the gene *JAZ13* [19]. Also, the lncRNA *ARTA* controls transcription through its ability to capture SAD2, which blocks the nuclear transport of the repressor MYB7. This prevents MYB7 from inhibiting ABI5, allowing its expression [20].

The regulatory function of lncRNAs in mRNA transcription occurs through their ability to bind directly with DNA and chromatin and transcriptional machinery

components. How they selectively target one gene among closely related homologs or neighboring loci remains unclear. However, lncRNA's structure, sequence complementarity, stability, and nuclear localization are likely to influence this specificity.

Alternative splicing

lncRNAs play a role in the alternative splicing (AS) of coding genes. By modulating AS, lncRNAs contribute to the fine-tuning of stress responses, support developmental timing, and enhance tissue-specific gene expression, thereby providing an additional layer of regulatory control. One well-characterized mechanism in eukaryotes by which lncRNAs interact with splicing factors is through sequestration, where the lncRNA acts as a molecular decoy, binding to splicing factors and subsequently limiting their availability [21] (Figure 1).

In Arabidopsis, the lncRNA *ASCO* is recognized by AS regulators known as nuclear speckle RNA-binding proteins (NSRs). It has been demonstrated that *ASCO* can hijack AS regulators to change splicing patterns in response to auxin by sequestering them away from their pre-mRNA targets [22]. Furthermore, *ASCO* was recently shown to interact with spliceosome core components [23]. *FLAIL* serves as an example of a trans-acting lncRNA that represses flowering by binding to its target genes through RNA−DNA interactions involving conserved sequence motifs. It interacts with the spliceosome complex and serves as a guide for AS of specific targets such as *LAC8* [24]. Another example is the circular RNA (circRNA) produced by back splicing of exon 6 in the *SEP3* gene in Arabidopsis [25]. The circRNA forms an R-loop with the DNA in the *SEP3* gene and promotes exon 6 skipping to generate a functional *SEP3* mRNA [25].

Plant lncRNAs actively influence the transcriptome by modulating pre-mRNA splicing. This function relies on DNA−RNA complementarity and/or the ability to interact with splicing factors. It is likely that lncRNAs (except for circRNAs) in this group need a specific secondary structure to recognize their partners.

The act of transcription

An underappreciated form of noncoding transcription is the case where the RNA produced is not the functional player rather it is the act of transcription that dictates a regulatory effect (Figure 1). Thus, the RNA molecules produced are rapidly degraded and difficult to detect with steady-state-level methods (i.e. RNA-seq). Recent advances in nascent transcription sequencing technologies (plant Native Elongation Transcript sequencing) have revealed thousands of such transcription events in Arabidopsis [26,27]. An isoform of *SVK* and the recently characterized lncRNA *SVALNA* repress *CBF1* and *CBF3* via an RNAPII collision mechanism, restricting convergently transcribing RNAPII complexes to reach the 3'-end of the genes [28,29]. Another example of this class is Transcriptional interference (TI), a process where noncoding transcription occurs over a gene's promoter and gene body [30]. TI changes the chromatin signature over the promoter and gene body to restrict proper start-site selection and mRNA generation. However, noncoding transcription does not have to be repressive. *PUPPIES*, a group of lncRNAs produced over the promoter of *DOG1*, activates the gene [31]. While the mechanism is not identified, transcription of *PUPPIES* alters RNAPII transcription dynamics over *DOG1* and allows for higher transcriptional burst sizes [31]. Recently, it has been shown that antisense transcription (where the RNA produced is degraded rapidly) is prevalent in Arabidopsis and promotes stress response [32,33] When antisense transcription was decreased, the transcription factors *ZAT5* and *BBX28* were not induced after cold exposure [33]. Similarly, decreasing antisense transcription at the *AAP1* locus renders the gene unresponsive to cold stress [32].

The activating role of noncoding transcription might represent a diverging function of plant lncRNAs compared to other eukaryote lncRNAs, and especially the link to environmental responsiveness in plants presents itself as an intriguing feature. How transcription of these sequences influences sense transcription is an obvious avenue for future studies. Overall, an important aspect of this research will be to understand the temporal and spatial occurrence of transcription at these loci.

Interaction with microRNAs

Within the intricate framework of gene regulation, lncRNAs influence the microRNAs' (miRNAs) activity to indirectly modulate gene expression at the post-transcriptional level. They primarily act as miRNA sponges and bind to specific miRNAs through partial sequence complementarity, thus preventing their interaction with mRNA targets, which is also known as endogenous target mimicry (eTM) [34,35] (Figure 1).

This regulatory phenomenon was first elucidated in Arabidopsis, where the degradation of PHO2, a key regulator of phosphate homeostasis, was prevented by miR399 due to its interaction with lncRNA, *Induced By Phosphate Starvation 1* (*IPS1*) [34]. Subsequently, similar eTM-based lncRNAs were identified in several plant species. For example, in tomato, lncRNA39896 binds to miR166b and acts as a molecular decoy that prevents its interaction with target transcripts *SlHDZ34* and *SlHDZ45* [36]. Similarly, in peach, the lncRNA1−miR6288b-3p−PpTCP4−PpD2 module controls branching [37].

circRNAs constitute a specific class of lncRNAs that can function as miRNA sponges in plants [38]. Although functional characterization is largely lacking, circRNAs have been predicted to function as miRNA sponges in a

wide range of plant species, such as trifoliate orange [39], cotton [40], and tomato [41]. A well-described case has been shown in rice, where *Os06circ02797* sponges OsMIR408 [42].

Beyond serving as miRNA decoys, lncRNAs have other regulatory roles. For instance, in Arabidopsis, the antisense transcripts of MIR398 (NAT398b and NAT398c) suppress the processing of pri-miR398, which results in reduced expression of miR398 [43]. Additionally, lncRNAs act as direct targets for miRNAs, which results in their cleavage. The cleaved lncRNAs undergo conversion into double-stranded RNA by RDR6 and are further processed into phased secondary small interfering RNAs (phasiRNAs) by Dicer-like proteins. Also, some lncRNAs serve as precursors for miRNAs, contributing to miRNA biogenesis. These miRNAs and phasiRNAs influence mRNA stability, resulting in gene silencing effects [44,45].

These dynamic interactions between lncRNAs and miRNAs depend on expression levels and structural compatibility. Despite emerging evidence, these interactions are largely unexplored, and it is still not well understood how plants control these interactions across different developmental stages or in response to environmental changes.

Concluding remarks

In this review, we have attempted to classify plant lncRNAs according to their function, albeit we still lack the exact molecular mechanism for many identified lncRNAs. A central theme of functional lncRNAs is their nuclear localization and their ability to regulate the chromatin environment adjacent to a coding gene, thereby influencing the expression. An important point is that lncRNAs can assert this function by the act of the transcription (the lncRNA is not stable) or by interacting with other proteins and/or DNA (the lncRNA is stable). Most lncRNAs function in *cis*, but some, more stable lncRNAs, can also function in *trans*. With the increased amount of lncRNA studies performed in plants, we can start to elucidate their molecular mechanisms, although more research in other plant species must complement the Arabidopsis work. Important future questions in the field include how lncRNAs recognize their partners (secondary structure of lncRNA and/or sequence complementarity), their evolution (there is poor cross-species conservation), their cell-specific expression patterns, and how plants use lncRNAs in a different manner compared to other eukaryotes, especially tied to development and the response to environmental stress.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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Data availability

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

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