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Functions of plants long non-coding RNAs

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ABSTRACT

Long non-coding RNAs (lncRNAs) have been emerged as important players for various biological pathways, including dosage compensation, genomic imprinting, chromatin regulation, alternative splicing and nuclear organization. A large number of lncRNAs had already been identified by different approaches in plants, while the functions of only a few of them have been investigated. This review will summarize our current understanding of a wide range of plant lncRNAs functions, and highlight their roles in the regulation of diverse pathways in plants.

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1. Introduction

The complexity of eukaryotic genome organization is revealed by high-throughput studies, which show that a great proportion of it encodes non-coding regulatory elements [1]. One class of these are the long non-coding RNAs (lncRNAs) — RNA molecules longer than 200 bp in length and lack protein-coding capacity. Originally, it was thought that production of lncRNAs is purely transcriptional "noise". However, the fact that lncRNAs levels are strictly regulated at transcriptional and post-transcriptional levels implies that lncRNAs could have important regulatory functions in complex organisms. Indeed, lncRNAs have been shown to play roles in key biological processes, including dosage compensation, genomic imprinting, X-chromosome inactivation, alternative splicing and nuclear organization in different organisms (reviewed in [2–8]).

The current researches on plant lncRNAs have linked them to the important biological processes such as gene silencing, flowering time regulation, abiotic stress responses and important developmental pathways. In this review, we will discuss recent research progresses in plant lncRNAs and their biological functions.

2. Genome wide identification of different types of lncRNAs in plants

Different approaches have been used to identify the genome wide lncRNAs in plants, and thousands of lncRNAs have been identified in *Arabidopsis* [9–18], rice [19–22], maize [23–25], *Medicago* [26], *Brassica* [27], *Populus trichocarpa* [28], wheat [29] and apple [30] (Table 1). Tiling array was used as a large-scale tool for identifying new transcripts in *Arabidopsis* before the Next-Generation Sequencing (NGS) technology was applied, and many lncRNAs had been found in this way. Recently strand specific RNA sequencing has been successfully implemented to identify the lncRNAs in *Arabidopsis*, rice and *Brassica*. Until now, the majority of plant lncRNAs have been identified through the analysis of ESTs, tiling array and NGS RNA-seq data, and can be classified into different types, e.g., sense, natural antisense, intronic and intergenic lncRNAs (Fig. 1 and Table 1, also see [31]). The large number of identified lncRNAs showed the specific expression profiles at different developmental stages and/or responded to different stresses. This data suggests that lncRNAs are widely spread in plants and may function in diverse biological processes. In spite of the large number of lncRNAs identified, the biological functions of only few of them have been investigated.

3. lncRNAs in regulation of *Arabidopsis Flowering Locus C*

The switch from vegetative stage to flowering is essential for plant reproduction. In *Arabidopsis*, there are multiple pathways that promote plant flowering, including plant hormone signaling, day length, light quality, and ambient temperature and others (reviewed in [32–38]). On the other hand, *Flowering Locus C* (*FLC*) represses the flowering process through the regulation of floral integrators [33], thus regulation of *FLC* expression is essential for flowering time control. To date, vernalization, autonomous, and FRIGIDA pathways have been identified to regulate the *FLC* expression (reviewed in [33,39,40]). Besides, non-coding RNAs, including small RNAs [41–43], antisense lncRNAs [44–50] and intronic lncRNA [51] are reported to be involved in these pathways to modulate the *FLC* expression. Among all these non-coding RNAs, a class of antisense lncRNAs named as *COOLAIR* had been

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Table 1
List of lncRNAs identified in plants.

Plant species	Approaches	Type(s) of lncRNAs	Numbers of lncRNAs	Year	Reference
Arabidopsis	In silico-EST	cis-NAT	1340	2005	[16]
	In silico-EST	trans-NAT	1320	2006	[14]
	In silico-EST	lncRNAs	76	2009	[18]
	Tiling array	lncRNAs	179	2009	[13]
	RNA-seq	lncRNAs	107	2011	[10]
	Tiling array	lincRNA	6480	2012	[12]
	RNA-seq	cis-NAT	2418	2013	[11]
	RNA-seq	Intermediate ncRNAs	838	2014	[17]
	Tiling array	sense-antisense pair	37238	2014	[15]
	RNA-seq	lncRNAs	955	2014	[9]
Rice	In silico-EST	sense-antisense pair	687	2003	[20]
	Microarray	sense-antisense pair	258	2003	[20]
	In silico-genome annotation	cis-NAT	344	2009	[22]
	In silico-genome annotation	trans-NAT	7142	2009	[22]
	RNA-seq	cis-NAT	3819	2012	[19]
	RNA-seq	lincRNAs	1624	2014	[21]
	RNA-seq	lncNATs	600	2014	[21]
Maize	In silico-EST	lncRNAs	1802	2012	[23]
	In silico-EST and RNA-seq	lncRNAs	20163	2014	[24]
	RNA-seq	lncRNAs	1724	2014	[25]
Medicago	In silico-genome annotation	lncRNAs	503	2007	[26]
Brassica	RNA-seq	cis-NATs	1301	2013	[27]
Populus trichocarpa	RNA-seq	lincRNAs	2542	2014	[28]
Wheat	Microarray and RNA-seq	lncRNAs	125	2011	[29]
Apple	Microarray	Sense/antisense	33201/21774	2014	[30]

thoroughly investigated for their importance in sense *FLC* regulation [44–50] through the autonomous and vernalization pathways.

3.1. Identification of lncRNA COOLAIR

In 2007, Swiezewski and co-workers identified two forms of small RNAs (30 nt and 24 nt, respectively) in the *FLC* 3′ end heterochromatic region (Fig. 2A) that are involved in the suppression of the *FLC* expression [43]. By detailed analysis, they found that some antisense RNA transcripts originated from this sRNA and heterochromatic region, and these transcripts could also be detected by whole-genome tiling array data [43,52]. Further analyzing the feature of these antisense transcripts by customized tilling array [49], they found that these transcripts cover the whole *FLC* gene locus (about 7 kb in size) and are terminated within the *FLC* promoter; are alternatively spliced and polyadenylated (classified as proximal and distal groups); and are up-regulated in the early vernalization stage (around 2 weeks of cold treatment, see also below, Fig. 2C). These antisense lncRNAs were named as *COOLAIR* (*cold induced long antisense intragenic RNAs*) based on the analogy of *HOTAIR* [53]. Interestingly, the RNA levels of sense *FLC* and antisense *COOLAIR* are correlated in most of flowering mutants and various treatments, but is disrupted during cold periods [44,46–50], indicating that *COOLAIR* may have important roles in *FLC* regulation in different pathways.

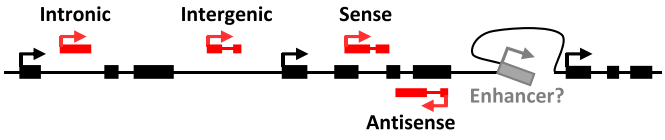

Fig. 1. Types of lncRNAs identified in plants. lncRNAs are classified according to their position of transcription with respect to the protein coding genes (black bricks). Long intergenic RNAs are transcribed between the protein coding genes while intronic lncRNAs are transcribed within the introns of the protein coding genes. Sense and antisense lncRNAs are transcribed from the sense and antisense strand of protein coding genes, respectively. Gray brick represents the putative plant enhancers, which have not been fully characterized in plants.

3.2. Function of COOLAIR in the autonomous pathway

Autonomous pathway is one of the important pathways that control *Arabidopsis* flowering time, and mainly through represses *FLC* gene expression (reviewed in [33,34,39]), and several key components in chromatin modification, RNA processing, and transcription elongation are essential for this pathway (see below [33,34,39]). Recent studies have shown that the autonomous pathway components work genetically and/or physically together to process lncRNA *COOLAIR* and thus in turn to regulate *FLC* expression and flowering time (Fig. 2A).

To understand the mechanism of an RNA binding protein FCA [54] in regulation of the autonomous pathway, Liu et al. started to screen the *suppressor of overexpressed FCA* (SOF) and identified the first suppressor FLD, the homolog to human H3K4 dimethylation demethylase LSD1 [55]. From further screens, two canonical 3′-processing factors CstF64 and CstF77 [46], a core spliceosome component PRP8 [47], and transcription elongation factor b (P-TEFb) like protein CDKC;2 [50] had been identified. Interestingly, detailed analysis showed that these SOF components are genetically essential for directing *COOLAIR* proximal polyadenylation [46,55], processing *COOLAIR* intron 1 splicing efficiency [47], and regulating *COOLAIR* expression [50]. These all contribute to induce the FLD-mediated H3K4me2 demethylation within *FLC* gene body (intron 1) [46,47,50,55], and thus leads to *FLC* repression (Fig. 2A). Similarly, FPA, another autonomous pathway factor, promotes *COOLAIR* proximal polyadenylation to repress *FLC* expression [45]. It is still elusive how proximal polyadenylation stimulates the FLD activity to repress *FLC*. Probably, the repression of distal *COOLAIR* transcription, the degradation products of distal forms of *COOLAIR*, or the degradation process itself, is the signal for recruiting FLD to *FLC* chromatin and decreases H3K4 dimethylation levels. Interestingly, recent data showed that exosome components RRP6L-1 and -2 are essential for repression of *FLC* through modulating different *COOLAIR* expression [56].

3.3. Function of COOLAIR in vernalization

For winter annual plants, exposure to the prolonged cold is essential for them to flower in spring. This process is called vernalization, which involves traditional epigenetic silencing mechanisms. In *Arabidopsis*, the main target of epigenetic silencing during vernalization is the *FLC*

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