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REVIEW
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From "Dark Matter" to "Star": Insight Into the Regulation Mechanisms of Plant Functional Long Non-Coding RNAs

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Long non-coding RNAs (lncRNAs) play a vital role in a variety of biological functions in plant growth and development. In this study, we provided an overview of the molecular mechanisms of lncRNAs in interacting with other biomolecules with an emphasis on those lncRNAs validated only by low-throughput experiments. LncRNAs function through playing multiple roles, including sponger for sequestering RNA or DNA, guider or decoy for recruiting or hijacking transcription factors or peptides, and scaffold for binding with chromatin modification complexes, as well as precursor of microRNAs or small interfering RNAs. These regulatory roles have been validated in several plant species with a comprehensive list of 73 lncRNA–molecule interaction pairs in 16 plant species found so far, suggesting their commonality in the plant kingdom. Such initial findings of a small number of functional plant lncRNAs represent the beginning of what is to come as lncRNAs with unknown functions were found in orders of magnitude more than proteins.

Keywords: plants, long non-coding RNAs, interaction, functional molecular, gene expression

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INTRODUCTION

Non-coding RNAs (ncRNAs), transcribed in over 90% of eukaryotic genomes of fungi, plants, and animals (Chekanova et al., 2007), were initially thought as "dark matter" in transcripts because their expressions are low, the sequences are poorly conserved, and the protein-coding potentials are absent (Palazzo and Koonin, 2020). With the advances in high-throughput sequencing and other experimental techniques, more ncRNAs begin to reveal their functional roles. In particular, they had been shown to play a key role in regulating the gene expressions at epigenetic, transcriptional, posttranscriptional, and posttranslational levels.

Long non-coding RNAs (lncRNAs) refer to those ncRNAs longer than 200 nucleotides (nt) in length (Rai et al., 2019; Palazzo and Koonin, 2020), as poorly conservative in sequence as other shorter ncRNAs (Chekanova, 2015). LncRNAs have been classified into three types according to their genomic locations: long intergenic ncRNAs (lincRNAs) in the intergenic regions, intronic ncRNAs (incRNAs) in the intronic regions, and natural antisense transcripts (NATs) from the antisense coding regions (Mattick and Rinn, 2015; Rai et al., 2019). Most lncRNAs are transcribed by RNA polymerase II (Pol II) or III (Pol III), and some could be produced by plant-specific RNA Pol IV and V (Wierzbicki et al., 2008). In this article, we summarized the molecular functions of plant lncRNAs discovered and validated by the low-throughput experiments with a specific focus on the relationship between lncRNAs and other biological macromolecules in regulating RNA activity, protein modification, and chromatin remodeling.

OVERVIEW

A large number of lncRNAs in plants were found by using transcriptome sequencing and bioinformatics analysis (Muers, 2011; Li et al., 2014, 2019; Hou et al., 2017; Yu T. et al., 2019). Several studies have summarized the bioinformatics tools and database resources for plant lncRNA identification and prediction (Jha et al., 2020; Waseem et al., 2020). However, until present, only a small number of these lncRNAs have been validated by the low-throughput experimental analysis. For example, Plant Long Non-Coding RNA Database version 2.0 (Jin et al., 2020) has 1,246,372 lncRNAs and predicted lncRNA targets in 80 species, and NONCODEV6 contains 94,697 lncRNAs in 23 plant species (Zhao et al., 2020). According to the experimentally validated functional lncRNA (EVLncRNA) predictions, nearly 30% of lncRNAs obtained by high-throughput sequencing have biological functions (Zhou et al., 2019). If lncRNAs are calculated on the order of millions, there are more than 200,000 predicted functional lncRNAs based on predictions (Zhou et al., 2019). By comparison, only 506 functional lncRNAs in 56 plant species are curated in the database of EVLncRNAs2.0 (Zhou et al., 2020). The majority of these EVLncRNAs belong to the model plant *Arabidopsis thaliana* (**Figure 1**). As shown in **Figure 2**, lncRNAs were found to regulate the downstream gene expression in *cis* or *trans* and play crucial roles in bud dormancy (Li et al., 2020), flowering time (Heo and Sung, 2011; Wang Z. W. et al., 2014; Kim et al., 2017), seedling photomorphogenesis (Wang Y. et al., 2014), root organogenesis (Ariel et al., 2014), sexual reproduction (Fan et al., 2016), gene silencing (Huang et al., 2011), and response to biotic and abiotic stress (Wunderlich et al., 2014; Kindgren et al., 2018; Zhao et al., 2018). In other words, the regulatory role of lncRNAs is extensive in eukaryotes (Long et al., 2017). The low-throughput experimental techniques include RNA fluorescence *in situ* hybridization (FISH), Northern blot, real-time quantitative polymerase chain reaction (RT-qPCR), overexpression, RNA interference (RNAi), clustered regularly interspaced short palindromic repeat-associated protein 9 (CRISPR/Cas9), RNA pull-down, RNA immunoprecipitation (RIP), and chromatin immunoprecipitation (ChIP) (Wu et al., 2020). **Table 1** provides the most up-to-date (November 30, 2020) list of all validated 73 lncRNA–molecule interaction pairs in 16 plant species that offer a glimpse of the molecular interaction network of functional lncRNAs in plant development and stress response. These interactions according to the interaction partners of lncRNAs are presented in the following sections.

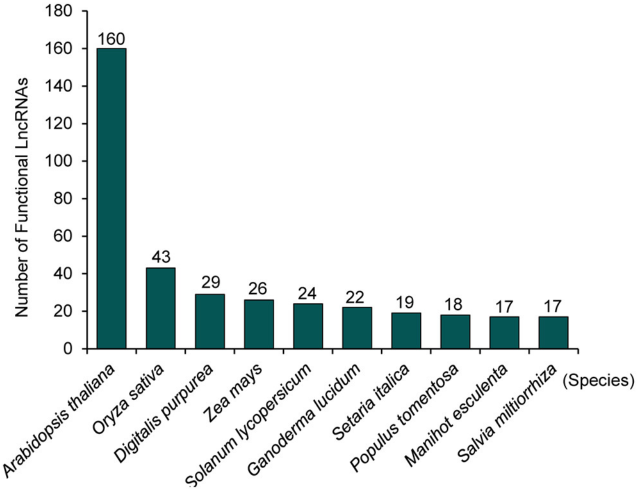

FIGURE 1 | Statistics of the number of functional lncRNAs in top 10 plant species based on the experimentally validated functional lncRNAs in plants, according to EVLncRNA2.0 (Zhou et al., 2020).

LONG NON-CODING RNA–RNA RELATIONS

Long Non-Coding RNA as an Endogenous Target Mimic to Repress microRNAs

The association between lncRNAs and small RNAs is perhaps the most reported relationship in plants. MicroRNAs (miRNAs) that are small ncRNAs (21–23 nt in length) play vital roles in diverse biological processes such as root development (Bazin et al., 2012), vegetative-to-reproductive transition (Yang et al., 2013), formation of phytohormones, and biotic/abiotic stress response (Yamamuro et al., 2016; Song X. et al., 2019). In principle, lncRNA could work as a "sponger" to adsorb a complementary miRNA to indirectly regulate the target genes of the miRNA. These lncRNAs are known as competitive endogenous RNAs (ceRNAs) or "endogenous target mimic (eTM)." In *Arabidopsis*, the lncRNA *IPS1* (*INDUCED BY PHOSPHATE STARVATION1*) is complementary to miR399, but it contains a mismatched loop to interrupt the pairing at the miRNA cleavage site (Franco-Zorrilla et al., 2007). As illustrated in **Figure 3A**, under the phosphate (Pi) starvation condition, *IPS1* is induced to sequester miR399. Sequestration of miR399 increases the transcriptional level of *miR399* target *PHO2* (encoding an E2 ubiquitin conjugase-related enzyme), which subsequently reduces the Pi content of the shoot (Franco-Zorrilla et al., 2007). The family members of *IPS1* have been identified in several species with the same functional mechanism as the eTM of miR399s, including *At4*, *At4-1*, *AT4-2*, and *AT4-3* in *A. thaliana* (Shin et al., 2006), *TPSI1* in *Solanum lycopersicum* (Liu et al., 1997), *Mt4* in barrel clover (Burleigh and Harrison, 1999), *PILNCR1* in maize (Du et al., 2018), *PDIL1* in *Medicago truncatula* (Wang et al., 2017), and *HvIPS1* and *HvIPS2* in *Hordeum vulgare* (Huang et al., 2011) (**Table 1**).

The above-mentioned eTM regulatory mechanism that occurs between other lncRNAs and miRNAs is conserved in different plant species and in biological pathway. As shown in **Table 1**, lncRNAs act as ceRNAs to sequestrate the silencing of miRNA for target genes, such as regulating leaf shapes in *Arabidopsis* (Wu et al., 2013), altering anthocyanin contents in *Hippophae rhamnoides* (Zhang et al., 2018), affecting the citrus fruit development (Ke et al., 2019), responding to auxin signal (Das et al., 2019), promoting jasmonic acid (JA) and methyl

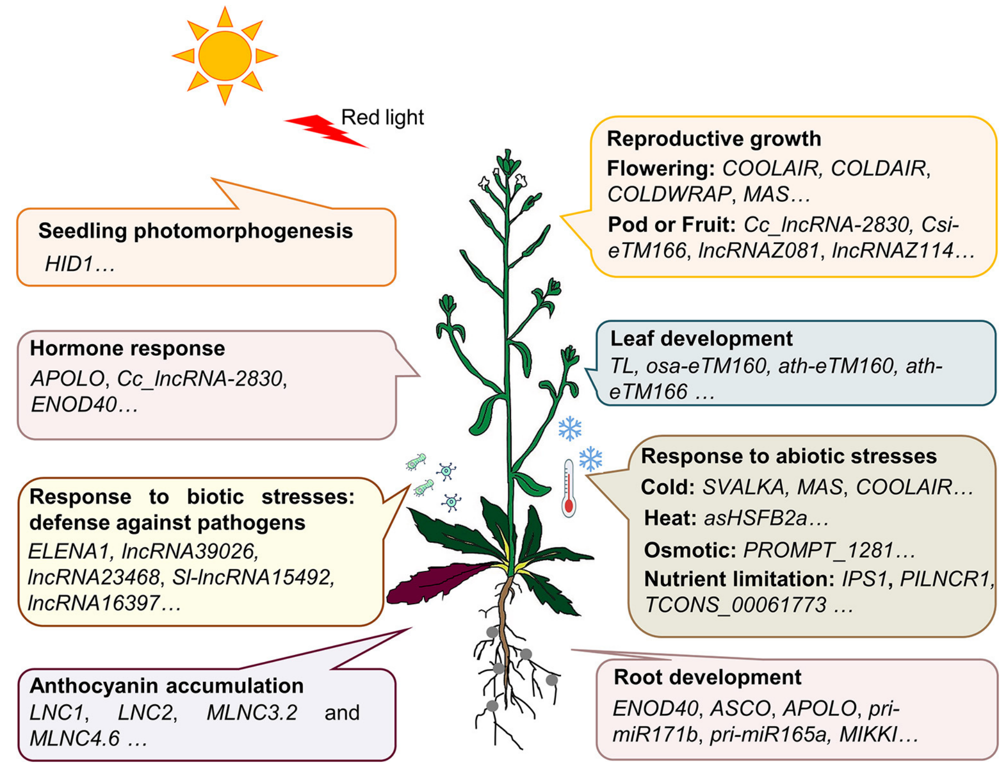

FIGURE 2 | LncRNAs play extensive roles in most aspects of plant growth and development. During plant growth and development, multiple lncRNAs are validated to play crucial roles. *HID1* plays an active role in seedling photomorphogenesis under continuous red light; *APOLO*, *Cc_lncRNA-2830*, and *ENOD40* were demonstrated to respond to the auxin treatment; *ELENA1*, *lncRNA39026*, and *lncRNA23468* enhance resistance to pathogen attacks; *COOLAIR*, *COLDAIR*, *COLDWRAP*, and *MAS* respond to cold, and involve in regulating the flowering time in vernalization; *TL*, *osa-eTM160*, *ath-eTM160*, and *ath-eTM166* affect the leaf shape; *SVALKA* regulates cold signal transduction; *asHSFB2a* is induced by heat stress and affects grain yield; *IPS1* and *PILNCR1* are induced by phosphate deficiency; *TCONS_00061773* respond to nitrate signal; *LNC1*, *LNC2*, *MLNC3.2*, and *MLNC4.6* are involved in anthocyanin accumulation; *ENOD40*, *APOLO*, *pri-miR171b*, *pri-miR165a*, and *MIKKI* are involved in root nodule organogenesis or lateral root development.

jasmonate (MeJA) biosynthesis and signal transduction pathways (Zhu et al., 2019), regulating rice root development (Cho and Paszkowski, 2017), and enhancing resistance to disease (Jiang et al., 2019; Hou et al., 2020).

Long Non-Coding RNA as a Precursor of phasiRNAs

The long non-coding RNAs that are binding with the complementary miRNA may lead to their cleavage to yield phased small-interfering RNAs (phasiRNAs). In eukaryote, lncRNAs or other RNAs are complemented and cleaved by miRNA to generate single-stranded RNAs first, and then to form double-stranded RNAs from the lysed RNA *via* RNA-dependent RNA polymerase, which are further processed into phasiRNA of 21–24 nt. Finally, phasiRNAs were loaded into AGONAUTE proteins for silencing RNA (Komiya, 2017). As shown in **Figure 3B**, the lncRNA *PMS1T*, encoded by *photoperiod-sensitive genic male sterility 1* (*Pms1*) locus in rice, is cleaved by miR2118 to generate 21-nt phasiRNAs. The abundance of phasiRNAs is associated with the photoperiod-sensitive male sterile (Fan et al., 2016; Komiya, 2017). Two other anther-specifically expressed lncRNAs, *Male Sterility-related PhasiRNA Precursor LincRNAs1* (*MSPPL1*) and *MSPPL2*, are also cleaved by miR2118 to yield phasiRNAs that play a role in the posttranscriptional regulation during meiosis in rice (Zhang et al., 2020). This mechanism is well-known in different plant development processes (**Table 1**); among these, *Cs1g09600* and *Cs1g09635* are cleaved by miR3954 to yield phasiRNAs, playing a role in the regulation of flowering in *Citrus sinensis* (Liu et al., 2017), *MuLnc1* is cleaved by miR3954 to produce phasiRNAs, disrupting the expression of the calmodulin-like protein gene *CML27* in *Morus multicaulis* (Gai et al., 2018), and *Sl-lncRNA15492*-miR482a-phasiRNAs affect the resistance to *Phytophthora infestans* in tomato (Jiang et al., 2020).

Long Non-Coding RNA as a Precursor of miRNA

In plants, the biogenesis of miRNAs is precisely controlled (Yu Y. et al., 2019). The production of miRNA undergoes a complex process in which *MIR* genes mainly located in the intergenic regions are first transcribed into primary miRNAs, then modified into the precursor miRNAs, forming miRNA duplexes, and finally forming mature miRNA to guide the posttranscriptional gene silencing (Sanei and Chen, 2015). Some lncRNAs act as the precursors of mature miRNAs (Liu

TABLE 1 | Functionally validated lncRNAs and their binding partners in plants.

Name	Species	Interaction target	Level of interaction	Biological functions	References
IPS1	*Arabidopsis thaliana*	miR399	RNA-RNA	Phosphate homeostasis	Franco-Zorrilla et al., 2007
At4	*Arabidopsis thaliana*	miR399	RNA-RNA	Phosphate homeostasis	Shin et al., 2006
At4-1	*Arabidopsis thaliana*	miR399	RNA-RNA	Phosphate homeostasis	Shin et al., 2006
At4-2	*Arabidopsis thaliana*	miR399	RNA-RNA	Phosphate homeostasis	Shin et al., 2006
At4-3	*Arabidopsis thaliana*	miR399	RNA-RNA	Phosphate homeostasis	Shin et al., 2006
Mt4	*Barrel clover*	miR399	RNA-RNA	Phosphate homeostasis	Shin et al., 2006
TPSI1	*Solanum lycopersicum*	miR399	RNA-RNA	Phosphate homeostasis	Liu et al., 1997
PDIL1	*Medicago truncatula*	miR399	RNA-RNA	Phosphate homeostasis	Wang et al., 2017
PILNCR1	*Zea mays*	miR399	RNA-RNA	Phosphate homeostasis	Du et al., 2018
HvIPS1	*Hordeum vulgare*	HvmiR399	RNA-RNA	Phosphate homeostasis	Huang et al., 2011
HvIPS2	*Hordeum vulgare*	HvmiR399	RNA-RNA	Phosphate homeostasis	Huang et al., 2011
lncRNA39026	*Lycopersicon esculentum*	miR-168a	RNA-RNA	Disease resistance	Hou et al., 2020
lncRNA23468	*Solanum lycopersicum*	miR-482b	RNA-RNA	Disease resistance	Jiang et al., 2019
LNC1	*Hippophae rhamnoides*	miR156a	RNA-RNA	Anthocyanin accumulation	Zhang et al., 2018
LNC2	*Hippophae rhamnoides*	miR828a	RNA-RNA	Anthocyanin accumulation	Zhang et al., 2018
MLNC3.2	*Malus domestica*	miRNA156a	RNA-RNA	Anthocyanin accumulation	Yang et al., 2019
MLNC4.6	*Malus domestica*	miRNA156a	RNA-RNA	Anthocyanin accumulation	Yang et al., 2019
csi-eTM166	*Citrus sinensis*	csi-miR166c	RNA-RNA	Fruit ripening	Ke et al., 2019
LTCONS_00026271	*Camellia sinensis*	novel_miR44	RNA-RNA	JA/MeJA synthesis and response	Zhu et al., 2019
LTCONS_00020084	*Camellia sinensis*	miR169d-5p_1	RNA-RNA	JA/MeJA synthesis and response	Zhu et al., 2019
Cc_lncRNA-2830	*Cajanus cajan*	miR-160h	RNA-RNA	Seed and pod development	Das et al., 2019
MIKKI	*Oryza sativa*	miR171	RNA-RNA	Root development	Cho and Paszkowski, 2017
eTM160	*Arabidopsis thaliana*	miR160	RNA-RNA	Leaf shape	Wu et al., 2013
eTM166	*Arabidopsis thaliana*	miR166	RNA-RNA	Leaf shape	Wu et al., 2013
Cs1 g09600	*Citrus sinensis*	miR-3954	RNA-RNA	Flowering time	Liu et al., 2017
Cs1 g09635	*Citrus sinensis*	miR-3954	RNA-RNA	Flowering time	Liu et al., 2017
MuLnc1	*Morus multicaulis*	miR-3954	RNA-RNA	Flowering time	Gai et al., 2018
PMS1T	*Oryza sativa*	miR2118	RNA-RNA	Male sterility	Fan et al., 2016; Komiya, 2017
MSPPL1	*Oryza sativa*	miR2118	RNA-RNA	Male sterility, meiosis	Zhang et al., 2020
MSPPL2	*Oryza sativa*	miR2118	RNA-RNA	Male sterility, meiosis	Zhang et al., 2020
lncRNA15492	*Solanum lycopersicum*	Sl-miR482a	RNA-RNA	Disease resistance	Jiang et al., 2020
lncRNAZ081	*Solanum lycopersicum*	miRNA6027	RNA-RNA	Ethylene response	Wang et al., 2018a
lncRNAZ114	*Solanum lycopersicum*	miRNA1919b	RNA-RNA	Ethylene response	Wang et al., 2018a
lncRNAZ114	*Solanum lycopersicum*	miRNA1919c	RNA-RNA	Ethylene response	Wang et al., 2018a
TCONS_00061773	*Solanum lycopersicum*	ptc-miR1448	RNA-RNA	Nitrogen deficient response	Chen et al., 2016
TCONS_00061773	*Solanum lycopersicum*	ptc-miR482a	RNA-RNA	Nitrogen deficient response	Chen et al., 2016
TL	*Oryza sativa*	*OsMYB60*	RNA-RNA	Leaf shape	Liu et al., 2018
asHSFB2a	*Arabidopsis thaliana*	*HSFB2a*	RNA-RNA	Heat stress response, gametophyte development	Wunderlich et al., 2014
lncRNA16397	*Solanum lycopersicum*	*SlGRX21*	RNA-RNA	Disease resistance	Cui et al., 2017
lncRNA16397	*Solanum lycopersicum*	*SlGRX22*	RNA-RNA	Disease resistance	Cui et al., 2017
HID1	*Arabidopsis thaliana*	*PIF3*	RNA-DNA	Seedling photomorphogenesis	Wang Y. et al., 2014
MAS	*Arabidopsis thaliana*	*MAF4*	RNA-DNA	Vernalization flowering	Zhao et al., 2018

(Continued)

TABLE 1 | Continued

Name	Species	Interaction target	Level of interaction	Biological functions	References
APOLO	*Arabidopsis thaliana*	*PID*	RNA-DNA	Auxin response; lateral root development	Ariel et al., 2014
APOLO	*Arabidopsis thaliana*	*WAG2*	RNA-DNA	Auxin response; lateral root development	Mas and Huarte, 2020
APOLO	*Arabidopsis thaliana*	*AZG2*	RNA-DNA	Auxin response; lateral root development	Mas and Huarte, 2020
LAIR	*Oryza sativa*	*LRK1*	RNA-DNA	Rice grain yield	Wang et al., 2018b
SVALKA	*Arabidopsis thaliana*	*CBF1*	RNA-DNA	Cold acclimation	Kindgren et al., 2018
APOLO	*Arabidopsis thaliana*	LHP1	RNA-Protein	Auxin response; lateral root development	Ariel et al., 2014
COOLAIR	*Arabidopsis thaliana*	FCA	RNA-Protein	Vernalization flowering	Tian et al., 2019
COLDAIR	*Arabidopsis thaliana*	PRC2	RNA-Protein	Vernalization flowering	Heo and Sung, 2011
COLDWRAP	*Arabidopsis thaliana*	PRC2 (CLF)	RNA-Protein	Vernalization flowering	Kim and Sung, 2017
ASL	*Arabidopsis thaliana*	AtRRP6L1	RNA-Protein	Flowering	Shin and Chekanova, 2014
MAS	*Arabidopsis thaliana*	MAS-WDR5a	RNA-protein	Vernalization flowering	Zhao et al., 2018
LAIR	*Oryza sativa*	OsMOF	RNA-Protein	Rice grain yield	Wang et al., 2018b
LAIR	*Oryza sativa*	OsWDR5	RNA-Protein	Rice grain yield	Wang et al., 2018b
ELENA1	*Arabidopsis thaliana*	MED19a	RNA-Protein	Disease resistance	Seo et al., 2017
ELENA1	*Arabidopsis thaliana*	FIB2	RNA-Protein	Disease resistance	Seo et al., 2019
ENOD40	*Medicago truncatula*	MtRBP1 (MtNSR1)	RNA-Protein	Nuclear-cytoplasmic relocalization, root nodules formation	Campalans et al., 2004
ENOD40	*Medicago truncatula*	AtNSRa	RNA-Protein	Nuclear-cytoplasmic relocalization	Bardou et al., 2014
ENOD40	*Medicago truncatula*	AtNSRb	RNA-Protein	Nuclear-cytoplasmic relocalization	Bardou et al., 2014
ASCO/lnc351	*Arabidopsis thaliana*	AtNSRa	RNA-Protein	Alternative splicing, root development	Bardou et al., 2014
ASCO/lnc351	*Arabidopsis thaliana*	AtNSRb	RNA-Protein	Alternative splicing, root development	Bardou et al., 2014
ASCO/lnc351	*Arabidopsis thaliana*	PRP8a	RNA-Protein	Alternative splicing, root development	Rigo et al., 2020
ASCO/lnc351	*Arabidopsis thaliana*	SmD1b	RNA-Protein	Alternative splicing, root development	Rigo et al., 2020
PROMPT_1281	*Populus simonii*	MYB	RNA-Protein	Osmatic stress response	Song Y. et al., 2019
MtENOD40	*Medicago truncatula*	MtSNARP1	RNA-peptide	Root nodules formation	Laporte et al., 2010
MtENOD40	*Medicago truncatula*	MtSNARP2	RNA-peptide	Root nodules formation	Laporte et al., 2010
GmENOD40	*Glycine max*	nodulin100	peptide A-Protein	Root nodules formation	Rohrig et al., 2002
GmENOD40	*Glycine max*	nodulin100	peptide B-Protein	Root nodules formation	Rohrig et al., 2002
pri-miR165a	*Arabidopsis thaliana*	miPEP165a	LncRNA encodes peptide	Root development	Lauressergues et al., 2015
pri-miR171b	*Medicago truncatula*	miPEP171b	LncRNA encodes peptide	Root development	Lauressergues et al., 2015
pri-miR858a	*Arabidopsis thaliana*	miPEP858a	LncRNA encodes peptide	Flavonoid biosynthesis	Sharma et al., 2020
pri-miR171d	*Vitis vinifera*	miPEP171d1	LncRNA encodes peptide	Adventitious root formation	Chen et al., 2020

et al., 2015; Yu Y. et al., 2019). In *Arabidopsis*, two lncRNAs, *npc83*, and *npc521*, are found to be the miRNA precursors for *MIR86lncRNA9A* and *MIR160C*, respectively (Ben Amor et al., 2009). The same phenomena are found in other plant species. *TCONS_00061773* are the precursors of ptc-miR1448 and ptc-miR482a, which involve in the defense mechanism to prevent nitrogen deficiency in *S. lycopersicum* (Chen et al., 2016) (**Figure 3C**). In tomato fruit, *lncRNAZ081* is the precursor of miRNA6027, and *lncRNAZ114* is the precursor of miRNA1919b and miRNA1919c (Wang et al., 2018a). In this study, we

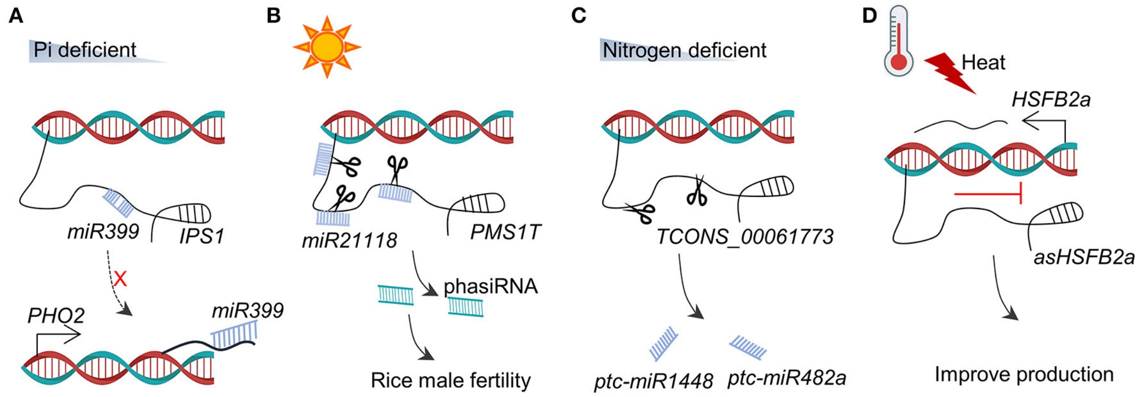

FIGURE 3 | The relationship between lncRNAs and RNAs. **(A)** Under Pi deficiency, *IPS1* serves as an eTM to bind with *miR399*, and prevents the interaction between *miR399* and *PHO2* mRNA. **(B)** *PMS1T* is sensitive to photoperiod and is targeted by *miR2118* to produce phasiRNA. **(C)** *TCONS_00061773* acts as the precursor of *ptc-miR1448* and *ptc-miR482a* in response to nitrogen deficiency. **(D)** Heat stress induces *asHSFB2a* and then represses *HSFB2a*.

described only miRNA precursors for those lncRNAs that were validated by the low-throughput experiments.

Long Non-Coding RNAs as Antisense Transcripts Co-Expressed With mRNAs

Some lncRNAs can be produced as antisense transcripts in the coding regions, and *cis*-regulate mRNA transcript through indirect physical interaction. As shown in **Figure 3D**, *asHSFB2a* in *A. thaliana* is a natural long non-coding antisense RNA of *HSFB2a* induced by heat stress (Wunderlich et al., 2014). The overexpressed *asHSFB2a* leads to an interrupt of *HSFB2a*, which subsequently improves the production in vegetative development (Wunderlich et al., 2014). Antisense lncRNAs were also found in *S. lycopersicum* and *Oryza sativa*. The antisense transcript of *SlGRX22*, *lncRNA16397*, upregulates the *SlGRX22* and *SlGRX21* expression and enhances the disease resistance of *P. infestans* by tomato (Cui et al., 2017). *TWISTED LEAF* (*TL*) in rice is an antisense transcript of R2R3-MYB transcription factor gene, namely, *MYB60* locus. The RNA interference and the overexpression experiments indicate that *TL cis*-suppresses the *MYB60* expression in regulating leaf blade flattening in rice by altering the chromatin structure (Liu et al., 2018).

LONG NON-CODING RNA–DNA INTERACTIONS

Long Non-Coding RNA–DNA Binding for Modulating Chromatin Loop Dynamics

Dynamic chromatin topology is closely associated with the gene expression patterns. In *Arabidopsis*, the lncRNA *AUXIN-REGULATED PROMOTER LOOP* (*APOLO*) was shown essential for the lateral root development by regulating the transcription level of auxin-responsive genes. *APOLO* controls these auxin-responsive genes in *cis* or *trans* by modulating chromatin loops (Mas and Huarte, 2020; **Figure 4A**). *APOLO* is activated by AUXIN RESPONSE FACTORS7 (ARF7) after treating with auxin and *cis*-activates the neighboring gene *PID* through formatting a chromatin loop with the promoter of *PID* by reducing H3K27me3 in the loop (Ariel et al., 2014). The opened loop is closed after *APOLO* generated from RNA Pol II further recruits polycomb repressive complex1 (PRC1) to deposit the DNA methylation on the genomic region of *APOLO-PID* (Ariel et al., 2014). *APOLO* transcripts can also regulate several distant target genes such as *WAG2* and *AZG2* through forming R-loops in *trans* (Ariel et al., 2020). *APOLO* recognizes its distant target genes by base complementarity through the formation of DNA–RNA duplexes. Two complementary TTCTTC boxes in *APOLO* RNA are confirmed to be essential for the formation of *APOLO*-target DNA loops (Ariel et al., 2020).

Long Non-Coding RNA–DNA Binding for Modulating Gene Transcriptions

The long non-coding RNAs can interact with DNA to regulate gene transcriptions. The knockdown of *HIDDEN TREASURE1* (*HID1*) (Wang Y. et al., 2014) in *Arabidopsis* displays elongated hypocotyls in continuous red light. ChIP-qPCR experiments revealed that *HID1* directly binds to the chromatin of the first intron of *PHYTOCHROME-INTERACTING FACTOR* 3 (*PIF3*) to repress its transcription in *trans* (Wang Y. et al., 2014). *HID1* is detected in nuclear. However, its protein partner is still unknown (**Figure 4B**). It should be noted that the sequence and secondary structure of *HID1* are highly conserved from moss to *Arabidopsis*, with a similar function in seedling photomorphogenesis (Wang Y. et al., 2014).

Transcription of Long Non-Coding RNA Modulates DNA Transcription

In plants, a novel transcriptional regulation mechanism of coding gene depends on the transcription of the adjacent lncRNA (Kindgren et al., 2018). The lncRNA *SVALKA*, found in the cold-sensitive region of the *Arabidopsis* genome, is the antisense transcript between *C-repeat/dehydration-responsive element binding factor3* (*CBF3*) and *CBF1*. RNA Pol II read-through transcription of *SVALKA* leads to the expression of

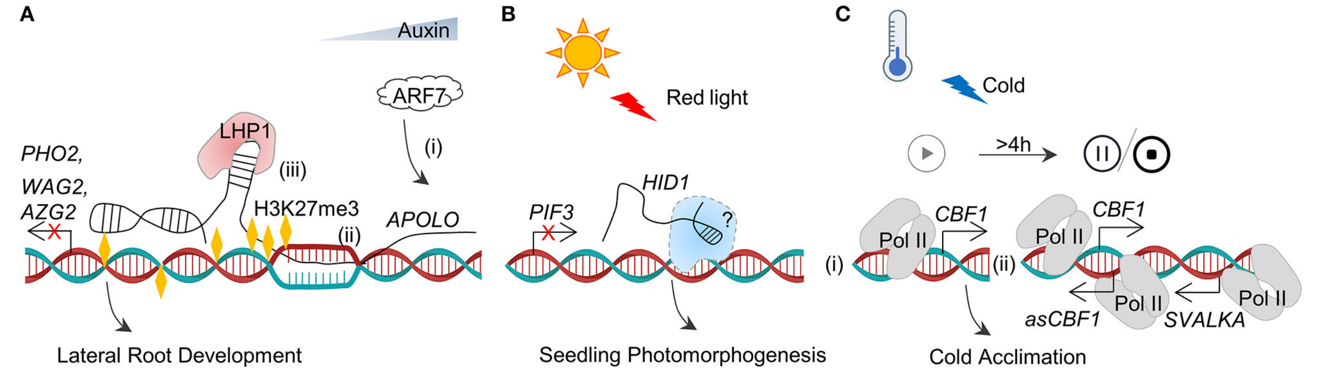

FIGURE 4 | LncRNA–DNA interactions. **(A)** (i) Upregulation of *APOLO* by ARF7 after auxin treatment, (ii) direct binding between *APOLO* and auxin-responsive genes chromatin through base complementarity to form R-loop in *cis* and *trans*. Expressions of these auxin-responsive genes contribute to the lateral development, and (iii) recruitment of LHP1 by *APOLO* to deposit H3K27me3 for closing the loop and then for silencing the *APOLO* target. **(B)** *HID1* binds to the proximal promoter of *PIF3* and represses its expression to modulate seedling photomorphogenesis. *HID1* may function by combining with proteins although the detail is still unknown. **(C)** (i) Sense *CBF1* is initiated by cold exposure, and the expression peaks after 4 h. (ii) Contemporaneously, *SVALKA* is induced in the antisense region of *CBF1*. RNA Pol II read-through transcription of *SVALKA* leads to the expression of *asCBF1* and an increase of RNA Pol II occupancy on strands. The collision of RNA Pol II stalls *CBF1* sense transcription.

antisense *CBF1* (*asCBF1*), and the cascade of *SVALKA*-*asCBF1* represses *CBF1* transcribing through RNA Pol II collision stemming, leading to maximize the low-temperature tolerance of plants with minimal adaptation changes (Kindgren et al., 2018) (**Figure 4C**).

LONG NON-CODING RNA–PROTEIN INTERACTIONS

Long Non-Coding RNAs as Guides for Recruiting Proteins

The long non-coding RNAs regulate the expression of genes by interacting with RNA-binding proteins. As mentioned earlier, after binding to the complementary DNA to form an R-loop, *APOLO* acts as a guide to recruit PRC1 component LIKE HETEROCHROMATIC PROTEIN1 (LHP1) to deposit the repressive histone marks (histone H3 Lys 27 trimethylation, H3K27me3) at the target chromatin and to repress the auxin-responsive gene transcription (Ariel et al., 2014; **Figure 4A**). The polycomb complex is recruited by lncRNAs during the process of vernalization-triggered flowering (Questa et al., 2016). The vernalization also induces three lncRNAs, such as *COLD INDUCED LONG ANTISENSE INTRAGENIC RNAs* (*COOLAIR*) (Baurle and Dean, 2006), *COLDWRAP* (Kim and Sung, 2017), and *COLD ASSISTED INTRONIC NON-CODING RNA* (*COLDAIR*) (Heo and Sung, 2011) which are derived from the antisense strand, the repressed promoter, and the first intron of *FLOWERING LOCUS C* (*FLC*), respectively (**Figure 5A**). These three lncRNAs involve in the deposition of H3K27me3 at *FLC* chromatin to repress *FLC* transcription (Kim and Sung, 2017). *COLDAIR* and *COLDWRAP* directly interact with PRC2, which catalyzes H3K27me3 (Heo and Sung, 2011; Kim and Sung, 2017; Kim et al., 2017), whereas *COOLAIR* binds to the protein FCA, which interacts with PRC2 subunit CURLY LEAF (CLF) to enrich H3K27me3 at *FLC* chromatin (**Figure 5A**). The protein phosphatase SSU72 physically interacts with FCA to antagonize the FCA binding with *COOLAIR* (Tian et al., 2019). In particular, an antisense lncRNA that derived by the same promoter of *COOLAIR* is independent on the vernalization in early-flowering *Arabidopsis* ecotypes. *ASL1* transcript physically associates with nuclear exosome component AtRRP6L1 (Callahan and Butler, 2008), maintaining H3K27me3 levels for silencing *FLC* (Shin and Chekanova, 2014).

Another cold-induced lncRNA is *MAS* that plays a regulatory role in the flowering time (Zhao et al., 2018). *MAS* is an NAT of the *MADS AFFECTING FLOWERING4* (*MAF4*) gene discovered in *Arabidopsis*, and it activates *MAF4* transcription involved in H3K4me3 deposition. Further assays showed that *MAS* binds to the locus of *MAF4* directly and recruits the COMPASS-like complexes (component WD repeat domain 5a, WDR5a) to enhance H3K4me3. The cold-induced formation of the MAS–WAR5a complex suppresses the premature flowering in vernalization (Zhao et al., 2018; **Figure 5A**). The interaction between lncRNAs and chromatin proteins modulates the chromatin 3D conformations of the neighboring or distant locus and affects the transcriptional activity in *cis* or *trans* (**Figures 4A, 5A**).

Long Non-Coding RNAs as Decoys for Hijacking Proteins

PROMPT_1281 is a promoter upstream transcript (PROMPT) lncRNAs, which is sensitive to osmotic stress in *Populus simonii*, through binding with MYBs transcription factors to interrupt them from interacting with DNA and lead to an increase in the expression of target genes in *cis* and *trans* (Song Y. et al., 2019; **Figure 5B**).

In *M. truncatula*, an lncRNA named as *MtENOD40* has a short open reading frame (sORF) and is important in root nodule organogenesis (Campalans et al., 2004). The functional analysis

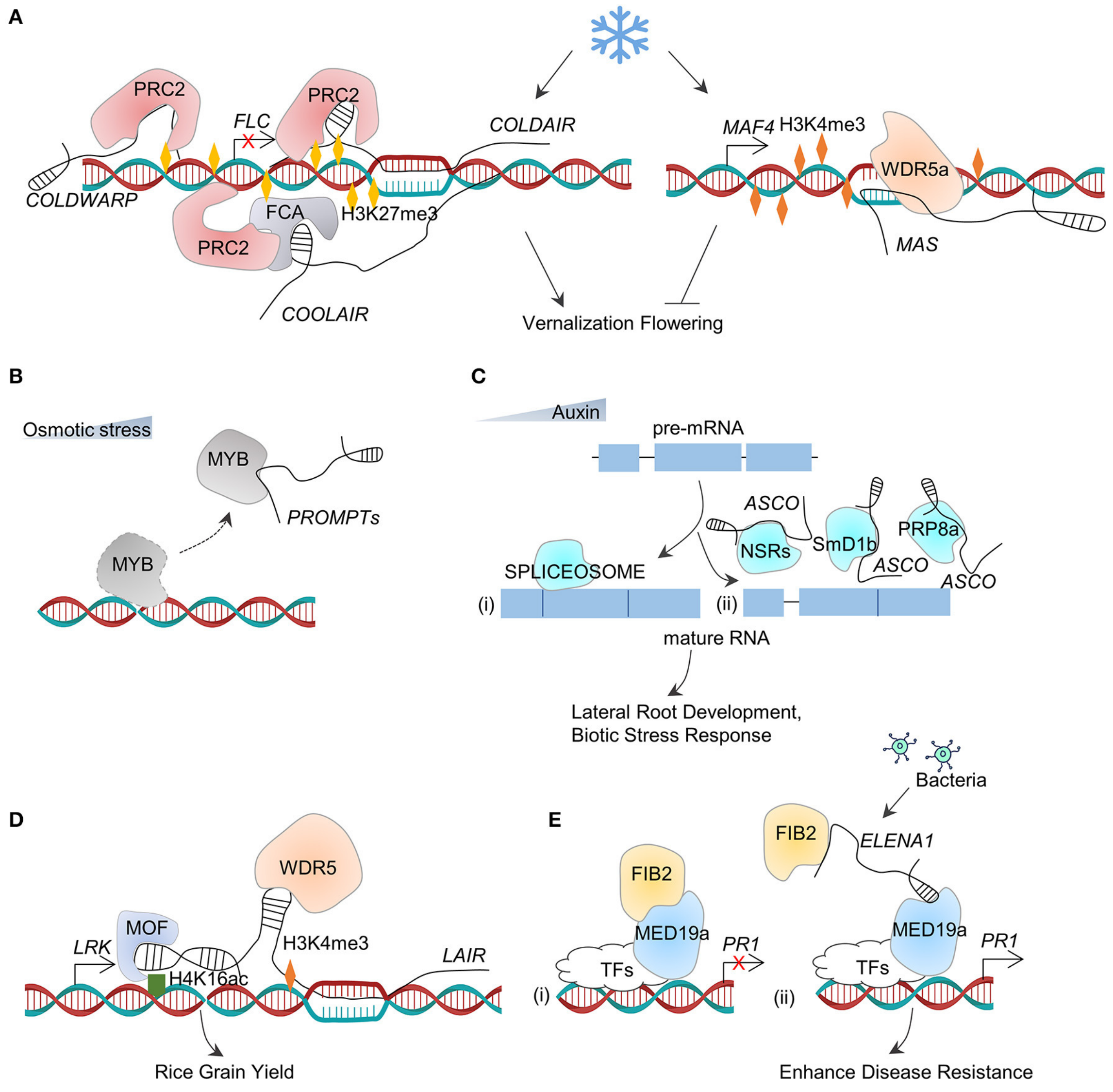

FIGURE 5 | LncRNA–protein interactions. **(A)** During vernalization, cold temperature induces *COLDAIR*, *COLDWARP*, and *COOLAIR.* Then, *COLDAIR* and *COLDWARP* recruit PRC2 to enrich H3K27me3 in the regulation region of *FLC* to repress its expression, whereas *COOLAIR* directly binds with FCA to recruit PCR2 and deposit H3K27me3 in the chromatin of *FLC*. At the same time, cold signal induces the expression of *MAS* and then recruits WDR5a to deposit H3K4me3 in the chromatin of *MAF4* to increase its expression. Downregulation of *FLC* and upregulation of *MAF4* ensure the accurate flowering time during vernalization. **(B)** Under osmotic stress, *PROMPTs* act as decoys to hijack the MYB transcription factors (TFs) for preventing their regular functions as TFs in regulating gene transcription. **(C)** During alternative splicing of pre-mRNA, multiple splicing factors including NSRs, SmD1b, and PRP8a binds (ii) or not (i) to *ASCO*, together with pre-mRNA to modulate transcriptome diversity dynamically. **(D)** *LAIR*, derived from the antisense transcript of *LRK*, directly interacts with the genomic region of *LRK* and then acts as a scaffold to recruit MOF and WDR5 to deposit H4K16ac and H3K4me3, respectively. This leads to the upregulation of *LRK* expression and increase of grain yield. **(E)** (i) In the absence of pathogen (bacteria) treatment, FIB2 directly interacts with MED19a, and this complex represses *PR1* expression; (ii) after the pathogen treatment, the transcription level of lncRNA *ELENA1* increases and then binds to FIB2 and MED19a. After FIB2 dissociates, MED19a continues to bind on the promoter of *PR1* and activate its expression.

indicates that *MtENOD40* can interact with *M. truncatula* RNA-binding protein 1 (MtRBP1, also named as *M. truncatula* Nuclear Speckles RNA-binding protein 1, MtNSR1). When *MtENOD40* expressed in root tissues, the *ENOD40*-MtRBP1 complex would relocate from the nucleus to the cytoplasm (Campalans et al., 2004). Interestingly, the *Arabidopsis* orthologs of MtRBP1 (i.e., AtNSRa and AtNSRb), when co-expressed with *MtENOD40*, also lead to the relocation of AtNSRs from the nucleus to the cytoplasm, indicating the conserved relocation activity of *MtENOD40* (Bardou et al., 2014). The above-mentioned AtNSR proteins participate in alternative splicing (AS) of pre-mRNA in *Arabidopsis* (Bardou et al., 2014). *Lnc351*, also called as *AS competitor long-non-coding RNA* (*ASCO-lncRNA*, *ASCO*), is induced by auxin. This lncRNA would

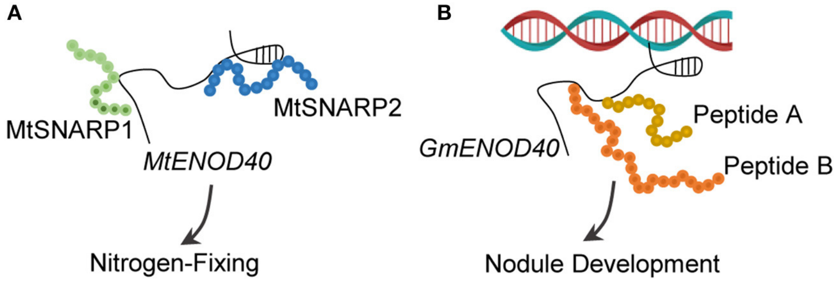

FIGURE 6 | LncRNA–peptide relations. **(A)** *MtENOD40* acts as a decoy to titrate two small peptides, namely, MtSNARP1 and MtSNARP2. Both peptides play a key role in establishing nitrogen-fixing symbiosis between *Medicago truncatula* and *Sinorhizobium meliloti*. **(B)** *GmENOD40* contains sORFs that encode two small peptides (Peptide A and Peptide B) of 12 and 24 amino acids each. Both peptides involve in the development of nitrogen-fixing nodules.

competitively bind AtNSRs with AS targets *in vitro* and *in vivo*, regulating transcriptome diversity in the formation of lateral root development (Bardou et al., 2014). Additionally, *ASCO* binds with multiple splicing factors including PRP8a and SmD1b and modulates the spliced genes in response to bacterial flagellin (Rigo et al., 2020) (**Figure 5C**). *ASCO* acts as an integrator through interacting with the spliceosome to dynamically modulate the transcriptome diversity.

Long Non-Coding RNAs as Scaffolds for Linking Multiple Proteins Together

The long non-coding RNAs can act as scaffolds to link multiple proteins together for forming the functional ribonucleoprotein complexes. The lncRNA *LAIR* (*LRK* Antisense Intergenic RNA) is derived from the antisense strand of neighboring gene *LRK* (leucine-rich repeat receptor kinase) cluster. Its overexpression leads to the upregulated expression of *LRK* genes and increased rice grain yields (Wang et al., 2018b). It was found that *LAIR* directly binds to the genomic regions of *LRK1* and functions as a scaffold to link histone modification proteins such as Males-absent-on-the-first (OsMOF) and OsWDR5 *in vivo*, which in turn gives a rise in the enrichment of H3K4me3 and H4K16 acetylation (H4K16ac) at chromatin to active *LRK1* (Wang et al., 2018b; **Figure 5D**).

Similarly, as a part of plant immune response, the lncRNA *ELF18-INDUCED LONG NON-CODING RNA 1* (*ELENA1*) activates *PATHOGENESIS-RELATED GENE1* (*PR1*) by directly binding with Mediator subunit 19a (MED19a) and negative transcription regulator FIBRILLARIN2 (FIB2) to enrich *MED19a* on *PR1* promoter (Seo et al., 2017). More specifically, an association of *ELENA1* with FIB2 (Seo et al., 2019) hinders the inhibitory effect of FIB2 on *PR1* and allows the accumulation of more MED19a on *PR1* promoter to activate the gene expression (**Figure 5E**).

LONG NON-CODING RNA–PEPTIDE RELATIONS

Long Non-Coding RNA–Peptide Interactions

In addition to interacting with RNA-binding proteins, *MtENOD40* was found to bind and repress two small nodulins, namely, Small Nodulin Acidic RNA-Binding Protein1 (MtSNARP1) and MtSNARP2 (Laporte et al., 2010). SNARPs are acidic peptides and are involved in the nitrogen-fixing symbiosis between *M. truncatula* and *Sinorhizobium meliloti* (**Figure 6A**). However, the interaction between MtSNARPs and *MtENOD40* in cytoplasm, as well as the functional role of MtRBP1 in cytoplasm require further studies.

Long Non-Coding RNA-Coding Peptides

The long non-coding RNAs typically lack the protein-coding potential. However, some lncRNAs were found to code peptides. Soybean *ENOD40* could produce two small peptides of 12 and 24 amino acids long, both of which bind to a subunit of sucrose synthase nodulin 100 for modulating sucrose use in nitrogen-fixing nodules (Rohrig et al., 2002; **Figure 6B**). Another example of lncRNA-coding peptides is pri-miRNAs, which are primary transcripts of miRNAs. The *pri-miR171b* of *M. truncatula* and the *pri-miR165a* of *Arabidopsis* contain sORFs that code the peptides miPEP171b and miPEP165a, respectively (Lauressergues et al., 2015). Increasing the expression levels of miPEP171b and miPEP165a alters the accumulation of miR171b and miR165a, reduces the lateral root development, and promotes the primary root growth (Lauressergues et al., 2015). A similar mechanism has been reported in other life processes, such as those involved in miPEP858a encoded by *pri-miR858a* to modulate flavonoid biosynthesis in *Arabidopsis* (Sharma et al., 2020) and miPEP171d1 encoded by *pri-miR171d* to accumulate miR171d and regulate adventitious root formation in *Vitis vinifera* (Chen et al., 2020), indicating the universality of this mechanism in plants (Prasad et al., 2020).

FUTURE DIRECTIONS

The finding of plant lncRNAs and their functional mechanisms is still in its early phase, and all the experimentally validated interaction pairs in plants are shown in **Table 1**. Although a large number of plant lncRNAs with unknown functions have been suggested by high-throughput sequencing, not all of them are functional. So far, only a small number of lncRNAs have been analyzed by the low-throughput biochemical and molecular biology functional assays. In fact, only 506 functional lncRNAs and 41 interactions of lncRNAs biomolecules in 56 plant species have been recorded in the recent update of the database for EVLncRNAs (https://www.sdklab-biophysics-dzu.net/EVLncRNAs2/) (Zhou et al., 2020). These data are only a tiny fraction of what can be possibly found. More experiments are needed to expand our knowledge in plant lncRNAs. Many questions that are to be addressed are as follows:

- What are the patterns in the secondary structure of lncRNAs in recognizing interacting molecules?
- What are the key sequence or structural factors that affect lncRNA functions?
- What is the degradation mechanism of lncRNAs in organisms?

These questions highlight the importance of RNA structures in providing functional clues. Recent advances in deep learning of protein structure prediction (Senior et al., 2020) and RNA secondary structure (Singh et al., 2019) highlight the importance of huge data in structure and function prediction. However, unlike proteins, the RNA structural and functional data remain scarce. As a result, the power of deep learning is quite limited until more data are available.

CONCLUSION

As illustrated in **Figure 2**, functional lncRNAs identified so far respond to the plant development signals, which act as regulators in plant growth and development in association with other macromolecules. LncRNAs in plants can respond to a variety of signals, including light (Wang Y. et al., 2014), phytohormones (Ariel et al., 2020), salt (Qin et al., 2017), temperature (Wunderlich et al., 2014; Kindgren et al., 2018), deficiency of nutritions such as phosphorus (Franco-Zorrilla et al., 2007; Zhang et al., 2019), and biotic stresses such as pathogen infection (Hou et al., 2020).

Currently, plant lncRNAs were shown to function through the formation of eTM with miRNA to regulate the expression of miRNA target genes indirectly (**Figure 3A**), acting as decoys to hijack nucleic acids or proteins to prevent their functions (**Figures 3A**, **5B**), the recruitment of modified proteins to remodel chromatin status at the epigenetic level (**Figures 4A**, **5A**), or the linkage of macromolecules to form functional complexes (**Figures 5D,E**). Similar mechanisms of interaction between plant lncRNA and other macromolecules can be found in eukaryotes such as humans, mammals, insects, and even fungi (Quinn and Chang, 2016; Golicz et al., 2018; Kazimierczyk et al., 2020), further suggesting the conservation of biological evolution on the earth. It should be noted that lncRNA is a single-stranded RNA that can recognize the complementary RNA or DNA sequences. Although some tools have been developed to predict the potential complementary nucleic acid molecules of lncRNA, the low abundance of lncRNAs makes it necessary to be certain about their biological effects by conducting the low-throughput experiments.

Taken together, understanding the functions of plant lncRNAs is just at the beginning stage. Model plants such as *A. thaliana* and *O. sativa* are the most studied plants (**Figure 1**). Significantly more studies are needed to cover the ocean of lncRNAs with unknown structures and functions. These fundamental studies are practically important because these lncRNAs are implicated in plant yield and quality and disease resistance. According to the current experimental identification technology, such as CRISPR/Cas9, RNAi, and loss and gain functions, the rate of functional lncRNA verified by the biological experiments is ∼600 per year (Zhou et al., 2020). It will be a long journey to fully understand the role of the massive amount of potential functional lncRNAs in the living organisms. Moreover, the growth of new high-throughput lncRNAs is accelerating. Thus, it is time to shed more light on the lncRNA "dark matter" to discover new "stars."

AUTHOR CONTRIBUTIONS

QC conceived the topic of the article. QC, KL, RY, PH, and ZC wrote the manuscript. BZ, YZ, and JW reviewed and revised the manuscript. All authors have directly contributed to the work and also read and approved the final published version.

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REFERENCES

Ariel, F., Jegu, T., Latrasse, D., Romero-Barrios, N., Christ, A., Benhamed, M., et al. (2014). Noncoding transcription by alternative RNA polymerases dynamically regulates an auxin-driven chromatin loop. *Mol. Cell* 55, 383–396. doi: 10.1016/j.molcel.2014.06.011

Ariel, F., Lucero, L., Christ, A., Mammarella, M. F., Jegu, T., Veluchamy, A., et al. (2020). R-Loop mediated trans action of the APOLO long noncoding RNA. *Mol. Cell* 77, 1055–1065.e1054. doi: 10.1016/j.molcel.2019.12.015

Bardou, F., Ariel, F., Simpson, C. G., Romero-Barrios, N., Laporte, P., Balzergue, S., et al. (2014). Long noncoding RNA modulates alternative splicing regulators in Arabidopsis. *Dev. Cell* 30, 166–176. doi: 10.1016/j.devcel.2014.06.017

Baurle, I., and Dean, C. (2006). The timing of developmental transitions in plants. *Cell* 125, 655–664. doi: 10.1016/j.cell.2006.05.005

Bazin, J., Bustos-Sanmamed, P., Hartmann, C., Lelandais-Briere, C., and Crespi, M. (2012). Complexity of miRNA-dependent regulation in root symbiosis. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 367, 1570–1579. doi: 10.1098/rstb.2011.0228

Ben Amor, B., Wirth, S., Merchan, F., Laporte, P., d'Aubenton-Carafa, Y., Hirsch, J., et al. (2009). Novel long non-protein coding RNAs involved in *Arabidopsis* differentiation and stress responses. *Genome Res.* 19, 57–69. doi: 10.1101/gr.080275.108

Burleigh, S. H., and Harrison, M. J. (1999). The down-regulation of Mt4-like genes by phosphate fertilization occurs systemically and involves phosphate translocation to the shoots. *Plant Physiol*. 119, 241–248. doi: 10.1104/pp.119.1.241

Callahan, K. P., and Butler, J. S. (2008). Evidence for core exosome independent function of the nuclear exoribonuclease Rrp6p. *Nucleic Acids Res*. 36, 6645–6655. doi: 10.1093/nar/gkn743

Campalans, A., Kondorosi, A., and Crespi, M. (2004). Enod40, a short open reading frame-containing mRNA, induces cytoplasmic localization of a nuclear RNA binding protein in *Medicago truncatula*. *Plant Cell* 16, 1047–1059. doi: 10.1105/tpc.019406

Chekanova, J. A. (2015). Long non-coding RNAs and their functions in plants. *Curr. Opin. Plant Biol*. 27, 207–216. doi: 10.1016/j.pbi.2015.08.003

Chekanova, J. A., Gregory, B. D., Reverdatto, S. V., Chen, H., Kumar, R., Hooker, T., et al. (2007). Genome-wide high-resolution mapping of exosome substrates reveals hidden features in the *Arabidopsis* transcriptome. *Cell* 131, 1340–1353. doi: 10.1016/j.cell.2007.10.056

Chen, M., Wang, C., Bao, H., Chen, H., and Wang, Y. (2016). Genome-wide identification and characterization of novel lncRNAs in Populus under nitrogen deficiency. *Mol. Genet. Genomics* 291, 1663–1680. doi: 10.1007/s00438-016-1210-3

Chen, Q. J., Deng, B. H., Gao, J., Zhao, Z. Y., Chen, Z. L., Song, S. R., et al. (2020). A miRNA-encoded small peptide, vvi-miPEP171d1, regulates adventitious root formation. *Plant Physiol*. 183, 656–670. doi: 10.1104/pp.20.00197

Cho, J., and Paszkowski, J. (2017). Regulation of rice root development by a retrotransposon acting as a microRNA sponge. *Elife* 6:e30038. doi: 10.7554/eLife.30038

Cui, J., Luan, Y., Jiang, N., Bao, H., and Meng, J. (2017). Comparative transcriptome analysis between resistant and susceptible tomato allows the identification of lncRNA16397 conferring resistance to *Phytophthora infestans* by co-expressing glutaredoxin. *Plant J*. 89, 577–589. doi: 10.1111/tpj.13408

Das, A., Nigam, D., Junaid, A., Tribhuvan, K. U., Kumar, K., Durgesh, K., et al. (2019). Expressivity of the key genes associated with seed and pod development is highly regulated via lncRNAs and miRNAs in *Pigeonpea*. *Sci. Rep*. 9:18191. doi: 10.1038/s41598-019-54340-6

Du, Q., Wang, K., Zou, C., Xu, C., and Li, W. X. (2018). The PILNCR1-miR399 regulatory module is important for low phosphate tolerance in maize. *Plant Physiol*. 177, 1743–1753. doi: 10.1104/pp.18.00034

Fan, Y., Yang, J., Mathioni, S. M., Yu, J., Shen, J., Yang, X., et al. (2016). PMS1T, producing phased small-interfering RNAs, regulates photoperiod-sensitive male sterility in rice. *Proc. Natl. Acad. Sci. U.S.A*. 113, 15144–15149. doi: 10.1073/pnas.1619159114

Franco-Zorrilla, J. M., Valli, A., Todesco, M., Mateos, I., Puga, M. I., Rubio-Somoza, I., et al. (2007). Target mimicry provides a new mechanism for regulation of microRNA activity. *Nat. Genet*. 39, 1033–1037. doi: 10.1038/ng2079

Gai, Y. P., Yuan, S. S., Zhao, Y. N., Zhao, H. N., Zhang, H. L., and Ji, X. L. (2018). A novel LncRNA, MuLnc1, associated with environmental stress in mulberry (*Morus multicaulis*). *Front. Plant Sci*. 9: 669. doi: 10.3389/fpls.2018.00669

Golicz, A. A., Bhalla, P. L., and Singh, M. B. (2018). lncRNAs in plant and animal sexual reproduction. *Trends Plant Sci*. 23, 195–205. doi: 10.1016/j.tplants.2017.12.009

Heo, J. B., and Sung, S. (2011). Vernalization-mediated epigenetic silencing by a long intronic noncoding RNA. *Science* 331, 76–79. doi: 10.1126/science.1197349

Hou, X., Cui, J., Liu, W., Jiang, N., Zhou, X., Qi, H., et al. (2020). LncRNA39026 enhances tomato resistance to phytophthora infestans by decoying miR168a and inducing PR gene expression. *Phytopathology* 110, 873–880. doi: 10.1094/PHYTO-12-19-0445-R

Hou, X., Du, Y., Liu, X., Zhang, H., Liu, Y., Yan, N., et al. (2017). Genome-Wide analysis of long non-coding RNAs in potato and their potential role in tuber sprouting process. *Int. J. Mol. Sci*. 19:101. doi: 10.3390/ijms19010101

Huang, C. Y., Shirley, N., Genc, Y., Shi, B., and Langridge, P. (2011). Phosphate utilization efficiency correlates with expression of low-affinity phosphate transporters and noncoding RNA, IPS1, in barley. *Plant Physiol*. 156, 1217–1229. doi: 10.1104/pp.111.178459

Jha, U. C., Nayyar, H., Jha, R., Khurshid, M., Zhou, M., Mantri, N., et al. (2020). Long non-coding RNAs: emerging players regulating plant abiotic stress response and adaptation. *BMC Plant Biol*. 20:466. doi: 10.1186/s12870-020-02595-x

Jiang, N., Cui, J., Hou, X., Yang, G., Xiao, Y., Han, L., et al. (2020). Sl-lncRNA15492 interacts with Sl-miR482a and affects *Solanum lycopersicum* immunity against *Phytophthora infestans*. *Plant J*. 103, 1561–1574. doi: 10.1111/tpj.14847

Jiang, N., Cui, J., Shi, Y., Yang, G., Zhou, X., Hou, X., et al. (2019). Tomato lncRNA23468 functions as a competing endogenous RNA to modulate NBS-LRR genes by decoying miR482b in the tomato-phytophthora infestans interaction. *Hortic. Res*. 6:28. doi: 10.1038/s41438-018-0096-0

Jin, J., Lu, P., Xu, Y., Li, Z., Yu, S., Liu, J., et al. (2020). PLncDB V2.0: a comprehensive encyclopedia of plant long noncoding RNAs. *Nucleic Acids Res*. 49, D1489–D1495. doi: 10.1093/nar/gkaa910

Kazimierczyk, M., Kasprowicz, M. K., Kasprzyk, M. E., and Wrzesinski, J. (2020). Human long noncoding RNA interactome: detection, characterization and function. *Int. J. Mol. Sci*. 21:1027. doi: 10.3390/ijms21031027

Ke, L., Zhou, Z., Xu, X. W., Wang, X., Liu, Y., Xu, Y., et al. (2019). Evolutionary dynamics of lincRNA transcription in nine citrus species. *Plant J*. 98, 912–927. doi: 10.1111/tpj.14279

Kim, D. H., and Sung, S. (2017). Vernalization-Triggered intragenic chromatin loop formation by long noncoding RNAs. *Dev. Cell* 40, 302–312.e304. doi: 10.1016/j.devcel.2016.12.021

Kim, D. H., Xi, Y., and Sung, S. (2017). Modular function of long noncoding RNA, COLDAIR, in the vernalization response. *PLoS Genet*. 13:e1006939. doi: 10.1371/journal.pgen.1006939

Kindgren, P., Ard, R., Ivanov, M., and Marquardt, S. (2018). Transcriptional read-through of the long non-coding RNA SVALKA governs plant cold acclimation. *Nat. Commun*. 9:4561. doi: 10.1038/s41467-018-07010-6

Komiya, R. (2017). Biogenesis of diverse plant phasiRNAs involves an miRNA-trigger and dicer-processing. *J. Plant Res*. 130, 17–23. doi: 10.1007/s10265-016-0878-0

Laporte, P., Satiat-Jeunemaitre, B., Velasco, I., Csorba, T., Van de Velde, W., Campalans, A., et al. (2010). A novel RNA-binding peptide regulates the establishment of the MEDICAGO truncatula-sinorhizobium meliloti nitrogen-fixing symbiosis. *Plant J*. 62, 24–38. doi: 10.1111/j.1365-313X.2009.04121.x

Lauressergues, D., Couzigou, J. M., Clemente, H. S., Martinez, Y., Dunand, C., Becard, G., et al. (2015). Primary transcripts of microRNAs encode regulatory peptides. *Nature* 520, 90–93. doi: 10.1038/nature14346

Li, J., Hull, J. J., Liang, S., Wang, Q., Chen, L., Zhang, Q., et al. (2019). Genome-Wide analysis of cotton miRNAs during whitefly infestation offers new insights into plant-herbivore interaction. *Int. J. Mol. Sci*. 20:5357. doi: 10.3390/ijms20215357

Li, L., Eichten, S. R., Shimizu, R., Petsch, K., Yeh, C. T., Wu, W., et al. (2014). Genome-wide discovery and characterization of maize long non-coding RNAs. *Genome Biol*. 15:R40. doi: 10.1186/gb-2014-15-2-r40

Li, L., Liu, J., Liang, Q., Zhang, Y., Kang, K., Wang, W., et al. (2020). Genome-wide analysis of long noncoding RNAs affecting floral bud dormancy in pears in response to cold stress. *Tree Physiol*. 39, 1821–1837. doi: 10.1093/treephys/tpaa147

Liu, C., Muchhal, U. S., and Raghothama, K. G. (1997). Differential expression of TPS11, a phosphate starvation-induced gene in tomato. *Plant Mol. Biol*. 33, 867–874. doi: 10.1023/a:1005729309569

Liu, J., Wang, H., and Chua, N. H. (2015). Long noncoding RNA transcriptome of plants. *Plant Biotechnol. J*. 13, 319–328. doi: 10.1111/pbi.12336

Liu, X., Li, D., Zhang, D., Yin, D., Zhao, Y., Ji, C., et al. (2018). A novel antisense long noncoding RNA, TWISTED LEAF, maintains leaf blade flattening by regulating its associated sense R2R3-MYB gene in rice. *New Phytol*. 218, 774–788. doi: 10.1111/nph.15023

Liu, Y., Ke, L., Wu, G., Xu, Y., Wu, X., Xia, R., et al. (2017). miR3954 is a trigger of phasiRNAs that affects flowering time in citrus. *Plant J*. 92, 263–275. doi: 10.1111/tpj.13650

Long, Y., Wang, X., Youmans, D. T., and Cech, T. R. (2017). How do lncRNAs regulate transcription? *Sci. Adv*. 3:eaao2110. doi: 10.1126/sciadv.aao2110

Mas, A. M., and Huarte, M. (2020). lncRNA-DNA hybrids regulate distant genes. *EMBO Rep*. 21:e50107. doi: 10.15252/embr.202050107

Mattick, J. S., and Rinn, J. L. (2015). Discovery and annotation of long noncoding RNAs. *Nat. Struct. Mol. Biol*. 22, 5–7. doi: 10.1038/nsmb.2942

Muers, M. (2011). RNA: genome-wide views of long non-coding RNAs. *Nat. Rev. Genet*. 12, 742. doi: 10.1038/nrg3088

Palazzo, A. F., and Koonin, E. V. (2020). Functional long non-coding RNAs evolve from junk transcripts. *Cell* 183, 1151–1161. doi: 10.1016/j.cell.2020.09.047

Prasad, A., Sharma, N., and Prasad, M. (2020). Noncoding but CODING: Pri-miRNA into the action. *Trends Plant Sci*. 26, 204–206. doi: 10.1016/j.tplants.2020.12.004

Qin, T., Zhao, H., Cui, P., Albesher, N., and Xiong, L. (2017). A nucleus-localized long non-coding RNA enhances drought and salt stress tolerance. *Plant Physiol*. 175, 1321–1336. doi: 10.1104/pp.17.00574

Questa, J. I., Song, J., Geraldo, N., An, H., and Dean, C. (2016). Arabidopsis transcriptional repressor VAL1 triggers polycomb silencing at FLC during vernalization. *Science* 353, 485–488. doi: 10.1126/science.aaf7354

Quinn, J. J., and Chang, H. Y. (2016). Unique features of long non-coding RNA biogenesis and function. *Nat. Rev. Genet*. 17, 47–62. doi: 10.1038/nrg.2015.10

Rai, M. I., Alam, M., Lightfoot, D. A., Gurha, P., and Afzal, A. J. (2019). Classification and experimental identification of plant long non-coding RNAs. *Genomics* 111, 997–1005. doi: 10.1016/j.ygeno.2018.04.014

Rigo, R., Bazin, J., Romero-Barrios, N., Moison, M., Lucero, L., Christ, A., et al. (2020). The *Arabidopsis* lncRNA ASCO modulates the transcriptome through interaction with splicing factors. *EMBO Rep*. 21:e48977. doi: 10.15252/embr.201948977

Rohrig, H., Schmidt, J., Miklashevichs, E., Schell, J., and John, M. (2002). Soybean ENOD40 encodes two peptides that bind to sucrose synthase. *Proc. Natl. Acad. Sci. U.S.A*. 99, 1915–1920. doi: 10.1073/pnas.022664799

Sanei, M., and Chen, X. (2015). Mechanisms of microRNA turnover. *Curr. Opin. Plant Biol*. 27, 199–206. doi: 10.1016/j.pbi.2015.07.008

Senior, A. W., Evans, R., Jumper, J., Kirkpatrick, J., Sifre, L., Green, T., et al. (2020). Improved protein structure prediction using potentials from deep learning. *Nature* 577, 706–710. doi: 10.1038/s41586-019-1923-7

Seo, J. S., Diloknawarit, P., Park, B. S., and Chua, N. H. (2019). ELF18-induced long noncoding RNA 1 evicts fibrillarin from mediator subunit to enhance pathogenesis-related gene 1 (PR1) expression. *New Phytol*. 221, 2067–2079. doi: 10.1111/nph.15530

Seo, J. S., Sun, H. X., Park, B. S., Huang, C. H., Yeh, S. D., Jung, C., et al. (2017). ELF18-induced long-noncoding RNA associates with mediator to enhance expression of innate immune response genes in *Arabidopsis*. *Plant Cell* 29, 1024–1038. doi: 10.1105/tpc.16.00886

Sharma, A., Badola, P. K., Bhatia, C., Sharma, D., and Trivedi, P. K. (2020). Primary transcript of miR858 encodes regulatory peptide and controls flavonoid biosynthesis and development in *Arabidopsis*. *Nat. Plants* 6, 1262–1274. doi: 10.1038/s41477-020-00769-x

Shin, H., Shin, H. S., Chen, R., and Harrison, M. J. (2006). Loss of At4 function impacts phosphate distribution between the roots and the shoots during phosphate starvation. *Plant J* 45, 712–726. doi: 10.1111/j.1365-313X.2005.02629.x

Shin, J. H., and Chekanova, J. A. (2014). Arabidopsis RRP6L1 and RRP6L2 function in flowering locus C silencing via regulation of antisense RNA synthesis. *PLoS Genet*. 10:e1004612. doi: 10.1371/journal.pgen.1004612

Singh, J., Hanson, J., Paliwal, K., and Zhou, Y. (2019). RNA secondary structure prediction using an ensemble of two-dimensional deep neural networks and transfer learning. *Nat. Commun*. 10:5407. doi: 10.1038/s41467-019-13395-9

Song, X., Li, Y., Cao, X., and Qi, Y. (2019). MicroRNAs and their regulatory roles in plant-environment interactions. *Annu. Rev. Plant Biol*. 70, 489–525. doi: 10.1146/annurev-arplant-050718-100334

Song, Y., Xuan, A., Bu, C., Ci, D., Tian, M., and Zhang, D. (2019). Osmotic stress-responsive promoter upstream transcripts (PROMPTs) act as carriers of MYB transcription factors to induce the expression of target genes in Populus simonii. *Plant Biotechnol J*. 17, 164–177. doi: 10.1111/pbi.12955

Tian, Y., Zheng, H., Zhang, F., Wang, S., Ji, X., Xu, C., et al. (2019). PRC2 recruitment and H3K27me3 deposition at FLC require FCA binding of COOLAIR. *Sci. Adv*. 5:eaau7246. doi: 10.1126/sciadv.aau7246

Wang, T., Zhao, M., Zhang, X., Liu, M., Yang, C., Chen, Y., et al. (2017). Novel phosphate deficiency-responsive long non-coding RNAs in the legume model plant Medicago truncatula. *J. Exp. Bot*. 68, 5937–5948. doi: 10.1093/jxb/erx384

Wang, Y., Fan, X., Lin, F., He, G., Terzaghi, W., Zhu, D., et al. (2014). Arabidopsis noncoding RNA mediates control of photomorphogenesis by red light. *Proc. Natl. Acad. Sci. U.S.A*. 111, 10359–10364. doi: 10.1073/pnas.1409457111

Wang, Y., Gao, L., Li, J., Zhu, B., Zhu, H., Luo, Y., et al. (2018a). Analysis of long-non-coding RNAs associated with ethylene in tomato. *Gene* 674, 151–160. doi: 10.1016/j.gene.2018.06.089

Wang, Y., Luo, X., Sun, F., Hu, J., Zha, X., Su, W., et al. (2018b). Overexpressing lncRNA LAIR increases grain yield and regulates neighbouring gene cluster expression in rice. *Nat Commun* 9, 3516. doi: 10.1038/s41467-018-05829-7

Wang, Z. W., Wu, Z., Raitskin, O., Sun, Q., and Dean, C. (2014). Antisense-mediated FLC transcriptional repression requires the P-TEFb transcription elongation factor. *Proc. Natl. Acad. Sci. U.S.A*. 111, 7468–7473. doi: 10.1073/pnas.1406635111

Waseem, M., Liu, Y., and Xia, R. (2020). Long non-coding RNAs, the dark matter: an emerging regulatory component in plants. *Int. J. Mol. Sci*. 2286. doi: 10.3390/ijms22010086

Wierzbicki, A. T., Haag, J. R., and Pikaard, C. S. (2008). Noncoding transcription by RNA polymerase Pol IVb/Pol V mediates transcriptional silencing of overlapping and adjacent genes. *Cell* 135, 635–648. doi: 10.1016/j.cell.2008.09.035

Wu, H. J., Wang, Z. M., Wang, M., and Wang, X. J. (2013). Widespread long noncoding RNAs as endogenous target mimics for microRNAs in plants. *Plant Physiol*. 161, 1875–1884. doi: 10.1104/pp.113.215962

Wu, L., Liu, S., Qi, H., Cai, H., and Xu, M. (2020). Research progress on plant long non-coding RNA. *Plants* 9:408. doi: 10.3390/plants9040408

Wunderlich, M., Gross-Hardt, R., and Schoffl, F. (2014). Heat shock factor HSFB2a involved in gametophyte development of Arabidopsis thaliana and its expression is controlled by a heat-inducible long non-coding antisense RNA. *Plant Mol. Biol*. 85, 541–550. doi: 10.1007/s11103-014-0202-0

Yamamuro, C., Zhu, J. K., and Yang, Z. (2016). Epigenetic modifications and plant hormone action. *Mol. Plant* 9, 57–70. doi: 10.1016/j.molp.2015.10.008

Yang, L., Xu, M., Koo, Y., He, J., and Poethig, R. S. (2013). Sugar promotes vegetative phase change in *Arabidopsis thaliana* by repressing the expression of MIR156A and MIR156C. *Elife* 2:e00260. doi: 10.7554/eLife.00260

Yang, T., Ma, H., Zhang, J., Wu, T., Song, T., Tian, J., et al. (2019). Systematic identification of long noncoding RNAs expressed during light-induced anthocyanin accumulation in apple fruit. *Plant J*. 100, 572–590. doi: 10.1111/tpj.14470

Yu, T., Tzeng, D. T. W., Li, R., Chen, J., Zhong, S., Fu, D., et al. (2019). Genome-wide identification of long non-coding RNA targets of the tomato MADS box transcription factor RIN and function analysis. *Ann. Bot*. 123, 469–482. doi: 10.1093/aob/mcy178

Yu, Y., Zhang, Y., Chen, X., and Chen, Y. (2019). Plant noncoding RNAs: hidden players in development and stress responses. *Annu. Rev. Cell Dev. Biol*. 35, 407–431. doi: 10.1146/annurev-cellbio-100818-125218

Zhang, G., Chen, D., Zhang, T., Duan, A., Zhang, J., and He, C. (2018). Transcriptomic and functional analyses unveil the role of long non-coding RNAs in anthocyanin biosynthesis during sea buckthorn fruit ripening. *DNA Res*. 25, 465–476. doi: 10.1093/dnares/dsy017

Zhang, Y. C., Lei, M. Q., Zhou, Y. F., Yang, Y. W., Lian, J. P., Yu, Y., et al. (2020). Reproductive phasiRNAs regulate reprogramming of gene expression and meiotic progression in rice. *Nat. Commun*. 11:6031. doi: 10.1038/s41467-020-19922-3

Zhang, Z., Zheng, Y., Ham, B. K., Zhang, S., Fei, Z., and Lucas, W. J. (2019). Plant lncRNAs are enriched in and move systemically through the phloem in response to phosphate deficiency. *J. Integr. Plant Biol*. 61, 492–508. doi: 10.1111/jipb.12715

Zhao, L., Wang, J., Li, Y., Song, T., Wu, Y., Fang, S., et al. (2020). NONCODEV6: an updated database dedicated to long non-coding RNA annotation in both animals and plants. *Nucleic Acids Res*. 49, D165–D171. doi: 10.1093/nar/gkaa1046

Zhao, X., Li, J., Lian, B., Gu, H., Li, Y., and Qi, Y. (2018). Global identification of *Arabidopsis* lncRNAs reveals the regulation of MAF4 by a natural antisense RNA. *Nat. Commun*. 9:5056. doi: 10.1038/s41467-018-07500-7

Zhou, B., Ji, B., Liu, K., Hu, G., Wang, F., Chen, Q., et al. (2020). EVLncRNAs 2.0: an updated database of manually curated functional long non-coding RNAs validated by low-throughput experiments. *Nucleic Acids Res*. 46, D86–D91. doi: 10.1093/nar/gkaa1076

Zhou, B., Yang, Y., Zhan, J., Dou, X., Wang, J., and Zhou, Y. (2019). Predicting functional long non-coding RNAs validated by low throughput experiments. *RNA Biol*. 16, 1555–1564. doi: 10.1080/15476286.2019.1644590

Zhu, C., Zhang, S., Fu, H., Zhou, C., Chen, L., Li, X., et al. (2019). Transcriptome and phytochemical analyses provide new insights into long non-coding rnas modulating characteristic secondary metabolites of oolong tea (*Camellia sinensis*) in solar-withering. *Front. Plant Sci*. 10:1638. doi: 10.3389/fpls.2019.01638

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