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Interplay between miRNAs and lncRNAs: Mode of action and biological roles in plant development and stress adaptation

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A R T I C L E   I N F O

A B S T R A C T

Plants employ sophisticated mechanisms to control developmental processes and to cope with environmental changes at transcriptional and post-transcriptional levels. MicroRNAs (miRNAs) and long noncoding RNAs (lncRNAs), two classes of endogenous noncoding RNAs, are key regulators of gene expression in plants. Recent studies have identified the interplay between miRNAs and lncRNAs as a novel regulatory layer of gene expression in plants. On one hand, miRNAs target lncRNAs for the production of phased small interfering RNAs (phasiRNAs). On the other hand, lncRNAs serve as origin of miRNAs or regulate the accumulation or activity of miRNAs at transcription and post-transcriptional levels. Theses lncRNA-miRNA interplays are crucial for plant development, physiology and responses to biotic and abiotic stresses. In this review, we summarize recent advances in the biological roles, interaction mechanisms and computational predication methods of the interplay between miRNAs and lncRNAs in plants.

Contents

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1. Introduction

The expression of genes is often spatiotemporally controlled at transcriptional and post-transcriptional levels. Transcription factors and proteins that remodel and modify chromatins play crucial roles in regulating gene transcription [1,2]. During transcription, pre-mRNAs are subjected to processing such as capping, splicing and adenylation, which provide additional regulations of gene expression. After transcription, the levels and activities of RNAs can be further controlled through RNA modifications, non-coding RNAs (ncRNAs) and various protein factors [3-6]. In eukaryotes, over 90% RNA transcripts do not encode proteins, which are called ncRNAs [7,8]. Some of these ncRNAs are basal components of molecular machineries such as ribosome and spliceosome, while others are important riboregulators of gene expression named regulatory ncRNAs [6,9,10]. Based on the length, the regulatory ncRNAs are classified into long ncRNAs (lncRNAs, greater than 200 nt) and short ncRNAs, including microRNAs (miRNAs), small interfering RNAs (siRNAs) and piwi-interacting RNAs (piRNAs). These regulatory RNAs modulate a variety of biological processes from cell differentiation, organ size and shape determination, to immunity at transcriptional and/or post-transcriptional levels [9,11-13]. Interestingly, the emerging evidence has documented the complex interplay between lncRNAs and short ncRNAs on gene regulation in plants and other eukaryotes [14-16].

To date, thousands of ncRNAs have been identified in plants, such as Arabidopsis [17], rice [18], maize [19], wheat [20], soybean [21], tomato [22], brassica [23], and sorghum [24]. As the two important types of ncRNAs, miRNAs and lncRNAs play critical roles

in plant growth, development, biotic and abiotic stress responses such as floret development [25,26], male sterility [27,28] , flower time [29,30], grain yield [31,32], fruit ripening [33], leaf morphogenesis [34], trichome formation [35,36], stem elongation [37,38], cell wall biosynthesis [39,40], tillering [41], root architecture [42], nodule formation [43,44] and responses to fungal infection [45], bacterial infection [46], virus infection [47], nematode infection [48], drought [49], cold [50], heat [51], submergence [52,53], salt [54,55], light [56] and nutrient stresses [57-61] (Fig. 1). However, the functional significance and action mechanisms of these regulatory RNAs remain to be deciphered, especially in crops with large and complex genomes. In this mini-review, we will summarize the current advances in the biological functions and action modes of miRNAs and lncRNAs with a focus on their interplays in plants.

2. Biological roles and molecular mechanisms of miRNAs

miRNAs are short (20–24 nucleotides in length) ncRNAs. From interval of 2002 to 2020, 20,388 miRNAs have been annotated in 88 phylogenetically representative plant species [62]. Studies on some miRNAs show that miRNAs regulate almost every biological process of plants from the developmental transition to responses to biotic and abiotic stresses [12,63-66] (Fig. 1). We briefly summarize plant miRNA biogenesis, action and related regulatory mechanisms here, since these aspects of miRNAs have been nicely reviewed [67-71](Fig. 2). In plants, miRNAs mainly inhibit gene expression at the post-transcriptional level through directly targeting mRNA transcripts for cleavage or translational repression [72].
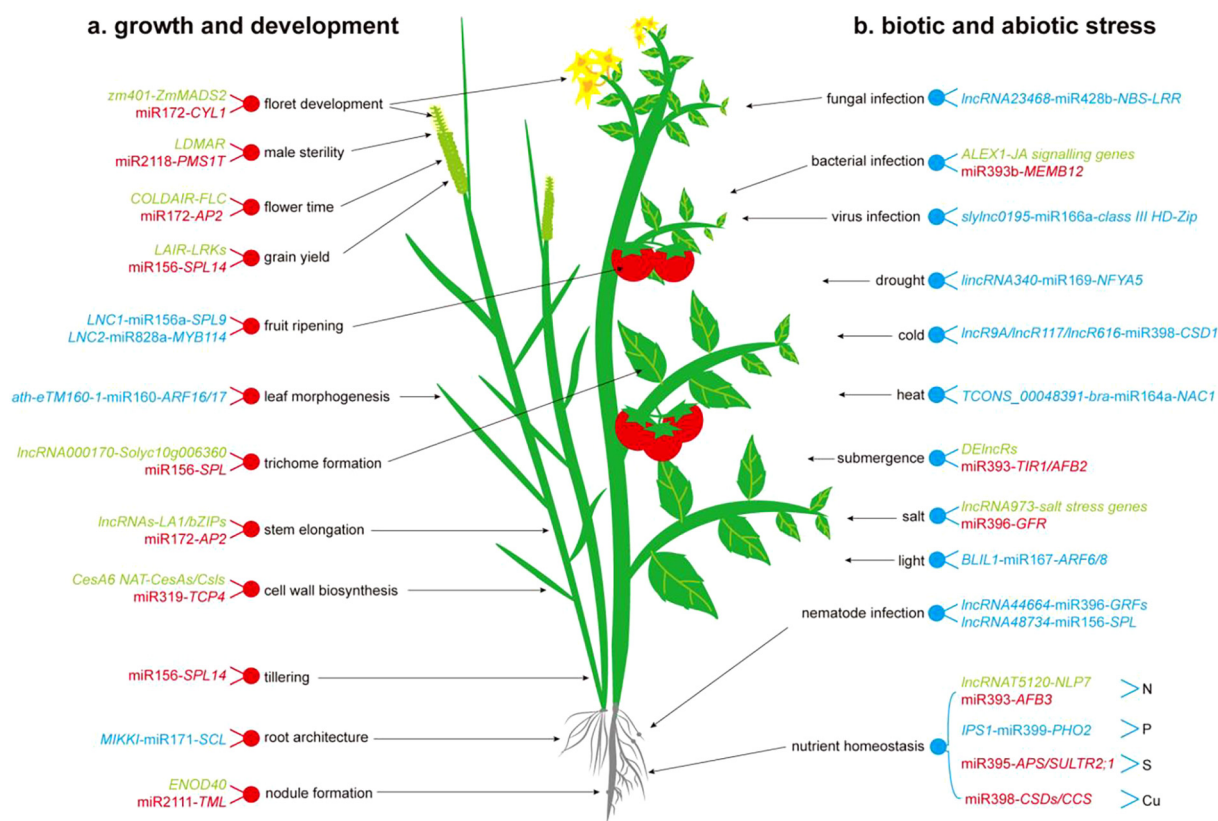
Fig. 1. The biological roles of lncRNAs, miRNAs and their interplay in plant growth and development, biotic and abiotic stress. (a) The representative lncRNAs (green), miRNAs (red) and their interactions (blue) regulate plant growth and development such as floret development [25,26], male sterility [27,28], flower time [29,30], grain yield [31,32], fruit ripening [33], leaf morphogenesis [34], trichome formation [35,36], stem elongation [37,38], cell wall biosynthesis [39,40], tillering [41], root architecture [42], and nodule formation [43,44]. (b) The representative lncRNAs (green), miRNAs (red) and their interactions (blue) are involved in biotic and abiotic stress responses such as fungal infection [45], bacterial infection [46], virus infection [47], nematode infection [48], drought [49], cold [50], heat [51], submergence [52,53], salt [54,55] , light [56], and nutrient stresses [57-61]. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Fig. 2. The action models of plant lncRNAs, miRNAs and their interplay in diverse biological processes. (a) LncRNAs i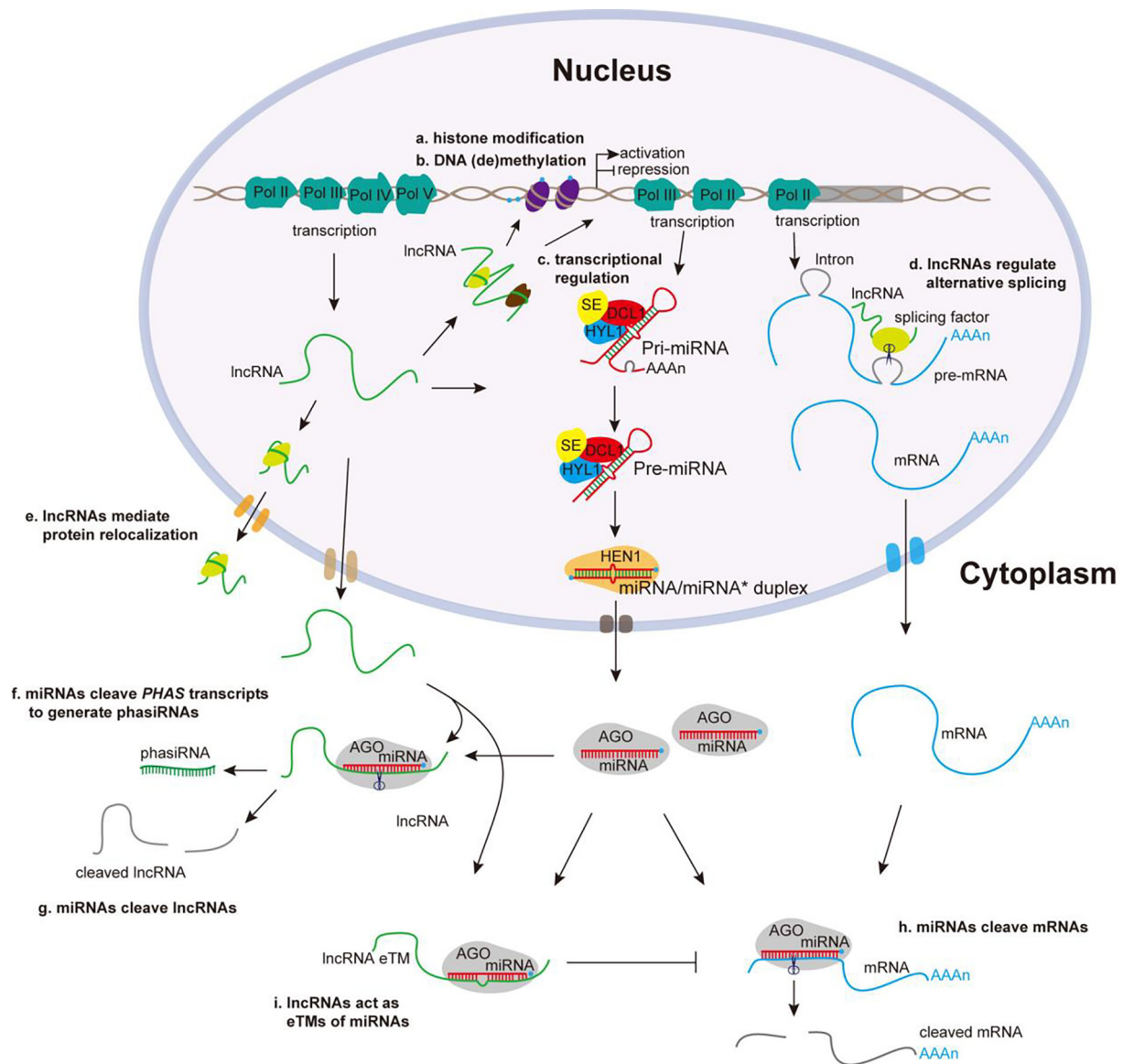nteract with histone modification complex to regulate histone modification [30,159]. (b) LncRNAs are involved in DNA (de)methylation to regulate gene transcription [27,160]. (c) LncRNAs regulate gene transcription by directly binding to proteins required for promoter activity of target genes [101,102]. (d) LncRNAs interact with alternative splicing factor such as RNA-binding protein to modulate alternative splicing (AS) patterns [97]. (e) LncRNAs mediate protein relocalizaion from nucleus to cytoplasm [161]. (f) miRNAs cleave *PHAS* transcripts to generate phasiRNAs [28,33]. (g) LncRNAs are cleaved by miRNAs leading to lncRNA degradation [109]. (h) MiRNAs cleave mRNAs to impact gene transcription [44,55]. (i) LncRNAs act as eTMs to inhibit miRNA effect on target mRNAs [42,59].

MiRNA biogenesis starts with transcription of primary miRNA transcripts (pri-miRNAs) from miRNA-encoding genes (*MIRs*) mainly by the DNA-dependent RNA polymerase II (Pol II) [72]. Pri-miRNAs harbor an imperfect stem-loop where the mature miRNAs are embedded. Following transcription, pri-miRNAs are processed into the miRNA/miRNA* duplex in nucleus mainly by the RNase III enzyme, DICER-LIKE1 (DCL1) [73]. Then the miRNA/miRNA* duplex is methylated by HUA ENHANCER 1 (HEN1) to improve its stability and then transported out of nucleus into cytoplasm [74-76]. MiRNA is incorporated into the ARGONAUTE 1 (AGO1) protein complex to form the miRNA-mediated silencing complex (miRISC) for repressing gene expression [77,78]. To ensure the efficiency and accuracy of miRNA biogenesis, a plethora of factors such as chromatin modifiers [79,80], transcriptional factors [81,82], RNA-associated proteins [83-85], and protein kinases [86] are employed to regulate the *MIR* transcription, pri-miRNA processing, RNA stability, and miRNA actions.

3. Biological roles and molecular mechanisms of lncRNAs

LncRNAs are a large family of non-coding RNAs with the length of more than 200nt. In plants, similar to mRNAs, Pol II-dependent lncRNA maturation requires capping, splicing and addition of a ploy-A tail, while Pol IV/V-dependent ones do not [87,88] (Fig. 2). LncRNAs are divided into three groups, long intergenic ncRNAs (no overlapping with protein-coding genes), long intronic ncRNAs (synthesized from intronic region), and natural antisense transcripts (NATs, synthesized from the opposite strand of the associated genes) according to their positions relative to protein-encoding genes in genomes [89]. In the past decades, great efforts have been made toward to the systematic identification and characterization of lncRNAs. For instance, using a reproducibility-based bioinformatics strategy, 6480 lncRNAs were identified from 200 transcriptome data sets in Arabidopsis [17]. Wang et al. identified 37,238 NATs, which are associated with 70% annotated mRNAs,

from Arabidopsis [90]. In cotton, 9240 lncRNAs from 21 tissues were identified by integrating multi-strategy RNA-seq data with a pipeline named plant full-length (PULL) [91]. Using the uniform annotation pipeline, 1,246,372 lncRNAs from 80 plant species have been collected according to 13,834 RNA-Seq datasets in Plant Long noncoding RNA Database (PLncDB) V2.0 [92]. Many lncRNAs identified by the prediction tools (see below) have been found to play important roles in plant growth and development. For example, in Arabidopsis, based on the prediction of a pipeline integrating Swiss-Prot database and CPC software [93,94], the lncRNA *MAS*, transcribed from *MADS AFFECTING FLOWERING4* (*MAF4*) locus, was found to be induced by cold and required for activating *MAF4* transcription by interacting with WDR5A during vernalization [95]. Arabidopsis lncRNA *T5120* obtained by the prediction of CPC and CNCI is activated by NLP7, the master nitrate regulatory transcription factor, and promotes plant growth through regulating nitrate assimilation [57].

Although a large number of lncRNAs have been identified, their biological roles and related molecular mechanisms only start to emerge in plants due to the low expression level compared with mRNAs or miRNAs. Studies show that lncRNAs regulate gene expression in both nucleus and cytoplasm via diversified action modes. In the nucleus, lncRNAs modulate gene expression through affecting chromatin remodeling, epigenetic modifications and alternative splicing [96-98] (Fig. 2). For instance, long intronic ncRNA *COLDAIR* (*COLD ASSISTED INTRONIC NONCODING RNA*) controls the transcription of *FLOWERING LOCUS C* (*FLC*), which is a key repressor for flowering time [30]. The nuclear-localized *COLDAIR* is transcribed from a locus within the *FLC* gene. It physically interacts with a component of polycomb repressive complex 2 (PRC2), and recruit PRC2 to the *FLC* locus for epigenetic repression during vernalization [30]. Interestingly, the antisense strand of *FLC* locus encodes another lncRNA named *COOLAIR*, which interacts with the RNA-binding protein FLOWERING CONTROL LOCUS A (FCA) to represses *FLC* transcription, accompanied with increased H3K27me3 and decreased H3K36me3 levels in cold condition [99,100]. The *COLDAIR-FLC* and *COOLAIR-FLC* modules represent one of the important roles of lncRNAs in the link of environmental signal and plant development. LincRNA *ELF18-INDUCED LONG-NONCODING RNA1* (*ELENA1*) is induced by the pathogen-associated molecular pattern (PAMP) [101]. *ELENA1* directly interacts with the Mediator subunit 19a (MED19a) and promotes its enrichment on *PATHOGENESIS-RELATED GENE 1* (*PR1*) promoter to increase the resistance to bacterial pathogen *Pseudomonas ayringae* pv. *tomato* DC3000 [102,103]. In the cytoplasm, lncRNAs can inhibit protein translation or act as miRNA mimics to inhibit miRNA activity (Fig. 2). *MIKKI* is a root-specific retrotransposon lncRNA in rice [42]. *MIKKI* binds and acts as miR171 decoy to inhibit its cleavage on *SCARECROW-Like* (*SCL*) mRNAs, leading to the increased cell elongation in root [42].

Despite of their biological importance, lncRNA biogenesis and related regulation mechanisms are still less known. Like the majority of *MIR* genes, lncRNAs are mostly transcribed by RNA Pol II, but sometimes by Pol III or the plant-specific RNA Pol IV/V [104,105]. In tomato, 187 lncRNAs are directly targeted by MADS-box transcription factor RIPENING INHIBITOR (RIN), which is a key factor required for tomato fruit ripening [106], suggesting the importance of transcription regulation in lncRNA biogenesis. In addition, cyclin-dependent kinase C (CDKC;2), a component of positive transcription elongation factor b (P-TEFb), is also involved in lncRNA biogenesis [107]. CDKC;2 can promote *COOLAIR* transcription by enhancing RNA Pol II Ser2 phosphorylation, thereby regulating flowering time in Arabidopsis [107]. Interestingly, the biogenesis of lncRNA and miRNA shares some key components in plants. SERRATE, CBP20 and CBP80, which are key components of miRNA biogenesis, act as regulators of lncRNA biogenesis and intron splicing

of some intron-containing lncRNAs [17]. However, DCL1, HYL1 and AGO1 are not required for lincRNA accumulation [17].

4. The interplay between miRNAs and lncRNAs

Recent studies have identified the interplay between miRNAs and lncRNAs. Besides serving as targets or origins of miRNAs, some lncRNAs are able to regulate the biogenesis and function of miRNAs (Fig. 2). The interactions between miRNAs and lncRNAs play important roles in regulating various biological process including development, nutrient abortion, biotic and abiotic stresses [108,109](Fig. 1).

4.1. LncRNAs are targets of miRNAs to generate phasiRNAs

LncRNA transcripts can be targeted by miRNAs to generate phased small interfering RNAs (phasiRNAs) [92] (Fig. 2). In phasiRNA biogenesis, RNAs including lncRNAs are first typically cleaved by 22 nt miRNAs. Then the RNA-DEPENDENT RNA POLYMERASE6 (RDR6) recruited by AGO1-RISC or AGO7-RISC converts the 3′ fragment into double-stranded RNAs (dsRNAs), which are further processed by a Dicer protein to generate duplexes of phasiRNAs [110-112]. The resulting phasiRNAs are loaded into AGO proteins and then direct AGOs to find their target transcripts [113]. In plants, ~15 years ago, a subset of lncRNAs that generate a class of phasiRNAs named *trans*-acting siRNAs (tasiRNAs) were first identified in Arabidopsis [110-112]. These lncRNAs are targeted by miRNAs including miR173, and miR390, respectively, to produce tasiRNAs [110-112]. Recently, some lncRNAs from reproductive organ were shown to produce reproductive phasiRNAs [114-117]. The targets for these phasiRNAs are largely unknown. However, they may regulate reproductive development, given their enrichment in reproductive tissues.

4.2. LncRNAs regulate pri-miRNA processing

Natural antisense transcripts (NATs) belong to a class of coding or ncRNAs that are divided into two clades, *cis*-NATs and *trans*-NATs, according to their derived region in genome [90]. Cis-NATs are transcribed from the opposite DNA strands at the same genomic locus, while *trans*-NATs originated from separate genomic loci [118]. Recent studies have revealed the role of *cis*-NAT in regulating pri-miRNA processing. *cis-NAT398b* and *cis-NAT398c* locate on the complementary strands to *MIR398b* and *MIR398c*, respectively [119]. Although the RNAs transcribed from these two loci encode proteins, Core-2/I-branching beta-1,6-N-acetylglucosaminyltrasfer ase and high-affinity nitrate transporter 2.7, they act as lncRNAs in the nucleus to impair the stability and processing of pri-miR398b/c without impacting their transcription [119]. Interestingly, pri-miR398b/c, but not the mature miR398b/c, directly activates *NAT398b/c* transcription in an unknown mechanism. By this feedback regulatory loop, plant fine-tunes thermotolerance [119], implying the complexity of miRNA-lncRNA interplay. *cis*-NATs are widely present in plants and often affect the expression level of the associated sense genes. Bioinformatic analysis has identified 22 *cis*-NATs that show reverse-complementary to *MIR* genes in Brassica [119], implying that the NAT-miRNA regulatory mechanism may be widely present.

Besides *cis*-NATs, some ncRNAs form dsRNA structures similar to that of pri-miRNAs to hijack the DCL1 complex, and thereby inhibit miRNA biogenesis. For instance, the transcripts derived from the short-interspersed elements (SINEs) can form a structure similar to pri-miRNAs, which in turn decoy HYL1 from pri-miRNA processing [120]. Another example is intron lariat RNAs, the byproducts derived from pre-mRNA splicing, which binds the

DCL1 complex and prevents pri-miRNA processing as the molecular sponge in Arabidopsis [121]. In addition, lncRNAs may impair microprocessor recognition and processing activity by forming lncRNA-miRNA precursor dimer. Actually, in human cells, some lncRNAs have been found to directly bind to miRNA precursors and block their processing to miRNAs by DICER complex [122,123]. However, this kind of miRNA processing-related lncRNAs has not been reported in plants to date.

4.3. LncRNAs act as target mimics of miRNAs

Target mimicry is one of the most important mechanisms of miRNA-lncRNA interplay, by which lncRNAs harboring endogenous target mimic (eTM) sites sequester miRNAs by sequence complementarity to inhibit their effects on target mRNA. Target mimicry is also described as miRNA decoy, miRNA sponge or competing endogenous RNA (ceRNA) in animals [124]. Arabidopsis *IPS1* (*INDUCED BY PHOSPHATE STARVATION 1*) is the first identified lncRNA which pairs with miR399 [59]. Both *IPS1* and miR399 are induced by Phosphate (Pi) deficiency. In contrast to the cleavage effect of target mRNA by miRNA, miR399-*IPS1* pairing contains a bulge which prevents miR399-mediated *IPS1* cleavage, and simultaneously cripples miR399-mediated *PHO2* degradation [59]. In maize, a novel lncRNA target of miR399, *PILNCR1*, is also required for low Pi tolerance [125], suggesting the lncRNA-miR399-*PHO2* regulatory module may be a widely mechanism in plant response to Pi deficiency.

Moreover, *lncRNA39026* binds miR168a and inhibits its function, which in turn improves tomato resistance to *Phytophthora infestans* [126]. These results suggest that lncRNAs may modulate various biological processes via hijacking miRNAs. Wu et al. developed a computational method and identified 36 and 189 potential eTMs in Arabidopsis and rice, respectively [34]. Since then, additional lncRNAs that potentially decoy miRNAs have been identified in maize [127], cassava[128], tomato [47,129,130], and melon [131]. However, the functional significance of these lncRNA-miRNA interactions still needs to be further analyzed.

4.4. LncRNAs inhibit miRNA expression

Some nuclear-localized lncRNAs regulate gene transcription through mediating chromatin modification. They serve as a bridge between transcription factors and chromatin [30,132,133]. Recent evidences show that the transcription of *MIRs* can also be regulated by lncRNAs in plants. Tomato Sl-miR482a functions as a negative regulator in immunity against *Phytophthora infestans* by repressing the expression of *NBS-LRR* genes [109]. Interestingly, *Sl-lncRNA15492* locates in the reverse strand of *Sl-MIR482a* and inhibits its transcription [109].

5. Methods to predict the interaction between lncRNAs and miRNAs

Despite the importance of the interplay between lncRNAs and miRNAs, a large portion of lncRNA-miRNA interactions remains to be identified. We summarize the available tools used to identify plant lncRNA-miRNA interactions here.

The prediction of lncRNA-miRNA interactions begins with the identification of miRNAs and lncRNAs. The miRNAs can be identified from the database such as miRBase [134], PmiREN [62], pmiRKB [135] and PMRD [136], while lncRNAs can be obtained from the lncRNA database such as NONCODE [137], lncRNAdb [138], GreeNC [139], PNRD [140], and PlncDB [92]. Once miRNAs and/or lncRNAs are identified, their interactions can be predicted with additional bioinformatic tools, such as TargetFinder [141],

TAPIR [142], psRobot [143], spongeScan [144], and PeTMbase [145]. Among these tools, TargetFinder, TAPIR and PmliPred require users to supply miRNA and potential target sequences. After sequence loading, these tools use various methods to find miRNA-target interactions. TargetFinder utilizes a FASTA local sequence alignment program to identify miRNA targets in plants by source code [140]. It should be noted that the FASTA program allows quick identification of targets but cannot find the RNA-miRNA duplexes having a lot of bulges and/or mismatches. Thus, it is less efficient in identifying lncRNA eTMs. In contrast, TAPIR uses both FASTA program and the precise RNAhybrid algorithm to identify miRNA targets [142]. The RNAhybrid algorithm finds the alignment between miRNA and lncRNA sequences that has the minimum free energy, which allows to predict less perfect match targets including lncRNA eTMs [142]. Indeed, using TAPIR, two lncRNA eTMs were identified to act in JA/MeJA biosynthesis in Oolong Tea [146], while 40 lncRNA eTMs of 15 miRNAs were predicted to be involved in early somatic embryogenesis in *Dimocarpus longan* Lour. [147]. Using python code, PmliPred is specially designed for predicting miRNA-lncRNA interactions in plants based on hybrid model and fuzzy decision [148]. In addition to the tools requiring user-prepared libraries, other ones perform prediction via the database-stored libraries. For instance, SpongeScan predicts miRNA response elements (MREs) within lncRNA eTMs, based on sequence complementary with preloaded miRNA library [144]. By cross-species conservation filter, Tarhunter identifies eTMs in 13 plant species [149]. Another tool called PsRobot discovers small RNAs with stem-loop precursors (e.g. miRNA) and their target transcripts via a Smith-Waterman algorithm up to 26 plant species [143]. A set of lncRNA eTMs identified by PsRobot have been shown to function in responses to tomato yellow leaf curl virus [47]. Based on the predefined scoring schema, PsRNATarget analyzes the complementary match between miRNAs and their target RNAs by evaluating target site accessibility [150]. Using PsRNATarget, *Lnc_973* and *lnc_253* have been found to serve as eTMs of ghr-miR399 and ghr-156e in cotton, respectively, to regulate salt stress response [151]. Using PsRobot and PsRNATarget, twelve lncRNAs were predicted to function as eTMs involved in Sneb821-induced tomato resistance to *M. incognita* [48].

Precision and recall rate are two important parameters to evaluate accuracy and sensitivity of the prediction results [152]. A comparison of prediction tools found that Targetfinder has a better efficiency in predicting miRNA targets in Arabidopsis, while PsRNATarget and TAPIR-hybrid perform well in non-Arabidopsis species [152]. The combination of different tools enhances the precision, but may reduce the sensitivity of prediction reducing the numbers of positive predictions [152,153]. For the precise and sensitive prediction, the algorithm of tools, multiple source of sequence and the co-expression miRNAs need to be taken into consideration [154]. Taken together, with the above tools and database, more lncRNA-miRNA interactions will be identified, which shall provide insight into the cross-talk among ncRNAs in various biological process.

6. Future perspectives

MiRNAs and lncRNAs play essential roles in regulating various biological processes. The interplay between miRNAs and lncRNAs not only provides additional layers of gene express, but also contributes to the complexity of biological systems. Technologies based on eTMs such as target MIMICs and short tandem target MIMICs have also been developed to study gene function and to improve agricultural traits such as grain yield and quality, resistance to environmental stresses [59,155-158]. However, studies on the interplay between miRNAs and lncRNAs are still in the

infant stage. Identification of the potential miRNA-lncRNA interaction in various plant species and in various physiological and developmental conditions is still a huge task. Moreover, among identified miRNA-lncRNA interactions, only a few have been analyzed in terms of biological significance. The detailed functional mechanisms for these interactions are still unclear. It will also be interesting to know if these miRNA-lncRNA interactions, related functions and mechanisms are conserved among different plant species. In addition, how various interplays between miRNAs and lncRNAs themselves are modulated at physiological and/or spatiotemporal levels and integrated into gene regulatory network are still largely unknown. Despite of these challenges, studies on the interplay between miRNAs and lncRNAs will be a rich source for exciting new discoveries, lead to a better understanding of gene regulation network and provide intellectual basis for improving important agricultural traits.

CRediT authorship contribution statement

Xiangxiang Meng: Writing - original draft, Writing - review & editing, Visualization. **Aixia Li:** Writing - original draft, Writing - review & editing. **Bin Yu:** Conceptualization, Supervision, Writing - original draft, Writing - review & editing. **Shengjun Li:** Conceptualization, Supervision, Writing - original draft, Writing - review & editing, Visualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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