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Role of long non-coding RNAs in rice reproductive development

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Rice is a staple crop, feeding over half of the global population. The future demand of population growth and climate change requires substantial rice improvement. Recent advances in rice genomics have highlighted the vital role of the non-coding part of the genome. The protein-coding regions account for only a tiny portion of the eukaryotic genome, and most of the genomic regions transcribe copious amounts of non-coding RNAs. Of these, the long non-coding RNAs, including linear non-coding RNAs (lncRNAs) and circular non-coding RNAs (circRNAs), have been shown to play critical roles in various developmental processes by regulating the expression of genes and functions of proteins at transcriptional, post-transcriptional and post-translational levels. With the advances in next-generation sequencing technologies, a substantial number of long non-coding RNAs have been found to be expressed in plant reproductive organs in a cell- and tissue-specific manner suggesting their reproductive development-related functions. Accumulating evidence points towards the critical role of these non-coding RNAs in flowering, anther, and pollen development, ovule and seed development and photoperiod and temperature regulation of male fertility. In this mini review, we provide a brief overview of the role of the linear and circular long non-coding RNAs in rice reproductive development and control of fertility and crop yield.

KEYWORDS

lncRNAs, circRNAs, rice, reproduction, anther, pollen, seed development

Introduction

Continuous advances in high throughput sequencing technologies coupled with the development of efficient bioinformatics tools have revealed the complexity of dynamic gene expression in plant cells (Kaufmann and Chen, 2017; García-Gómez et al., 2020; Alvarez et al., 2021). Transcriptional and post-transcriptional processes can generate diverse RNA molecules with or without protein-coding potential. Protein coding RNAs, or messenger RNAs (mRNAs), that carry the genetic code that can be translated to proteins comprise less than 2% of the transcriptome in a cell. The vast majority of RNAs are non-protein coding or non-coding RNAs (ncRNAs) with the potential to regulate

essential biological functions in various processes. Non-coding RNAs are diverse but based on their size and form; they can be classified into small ncRNAs, long non-coding RNAs (lncRNA), and circular RNAs (circRNAs) (Jarroux et al., 2017; Kaikkonen and Adelman, 2018; Panni et al., 2020). Recent studies have indicated that a subset of ncRNAs can encode small peptides or polypeptides with known or unknown functions (Choi et al., 2019; Kong et al., 2020).

lncRNAs are defined as transcripts with a length of over 200 nucleotides with no apparent protein-coding potential (Waseem et al., 2020). Based on the functional studies during the past decade, lncRNAs can be categorized as RNA molecules that exert their roles with their nucleotide sequences and structure independent of their potential genetic code (Wierzbicki et al., 2021). lncRNAs can be classified based on their genomic locations with coding regions: including intronic, intergenic, sense, and antisense directions lncRNAs. Compared to protein-coding RNAs, lncRNAs have certain unique characteristics, such as less sequence conservation, shorter length, and more tissue-specific expression (Golicz et al., 2018; Rai et al., 2019). lncRNAs modulate the expression of their neighboring or distal genes through various mechanisms (Lucero et al., 2021). For example, lncRNA ELF18-INDUCED LONG NONCODING RNA1 (ELENA1), which is expressed from the promoter region of the PATHOGENESIS-RELATED 1 (PR1) gene in Arabidopsis has been shown to activate and enhance the expression of PR1 in response to pathogen elicitors by directly interacting with core transcriptional machinery at the PR1 promoter (Seo et al., 2017). lncRNA ALTERNATIVE SPLICING COMPETITOR (ASCO) was shown to interact with nuclear speckle RNA-binding proteins (NSRs: alternative splicing regulators) to regulate gene expression by modulating the alternative splicing patterns of NSR target genes during plant development (Bardou et al., 2014). lncRNAs can also regulate the expression of distal genes by forming DNA-RNA duplexes or R-loops. APOLO (AUXIN-REGULATED PROMOTER LOOP) is an example of a lncRNA that can regulate the expression of several distal and independent genes in the Arabidopsis genome by targeting short complementary sequences and forming R-loops (Ariel et al., 2020). APOLO is also associated with regulating gene expression in response to Auxin through the formation of chromosome looping and epigenetic modifications (Ariel et al., 2014). lncRNAs can also control the gene expression either by acting as miRNA target mimicry or as precursors of miRNAs and other small RNAs such as phased secondary small interfering RNAs (phasiRNAs). In the target mimicry mechanism, lncRNAs perform their role by sponging miRNAs and sequestering them from repressing their mRNA targets (Borah et al., 2018). As the small RNA substrate, lncRNAs are cleaved by Argonaute complexes to generate miRNAs or phasiRNAs (Meng et al., 2021).

CircRNAs are another class of regulatory lncRNA molecules that arise from an uncanonical type of splicing named back-splicing, during which the spliceosome covalently joins an

upstream 3' splice site to a downstream 5' splice site to form circle RNAs with no 5' caps or 3' poly-A tails (Xiao et al., 2020). Like linear lncRNA, circRNAs have tissue-specific expression and can be transcribed from various genomic regions, including exons, introns, and intergenic regions (Guria et al., 2020). However, many identified circRNAs in most plant species were composed of exonic regions (Chu et al., 2020). CircRNAs mostly have a low abundance in the cell, but in some cases, they can accumulate to a high level, mostly due to their resistance to exonucleases (Liu and Chen, 2022). Studies in humans and animals have reported the involvement of circRNAs in many molecular processes, such as transcription, alternative splicing, translation, and miRNA sponging (Xiao et al., 2020; Guria et al., 2020; Liu and Chen, 2022). For example, exon-intron circRNAs abundant in the nucleus of human cells were associated with RNA polymerase II machinery and reported to positively regulate the expression of their parent genes through *cis*-acting regulatory roles (Li et al., 2015). CircRNAs can also regulate translation and cell division by interacting with proteins. CircRNA Poly(A)-Binding Protein Nuclear 1 (circPABPN1) has been shown to regulate the translation of its cognate mRNA by interacting with RNA-binding protein Human antigen R (HuR). CircPABPN1 could bind HuR and prevent HuR from binding PABPN1 mRNA, which resulted in the reduced translation of PABPN1 mRNA (Abdelmohsen et al., 2017). MiRNA sponging is probably one of the well-known functions of circRNAs in humans and animals. For example, CDR1as contains over 70 binding sites for miR-7, and the overexpression of CDR1as in human cells suppressed the activity of miR-7 significantly, indicating this circRNAs as miRNA sponging (Hansen et al., 2013; Memczak et al., 2013). In plants, circRNAs have been reported to be expressed at almost all stages of growth and development (Zhao et al., 2019). Although the exact molecular function of most identified circRNAs in plants remains to be explored, previous studies have suggested that circRNAs could have important functions during plant development and in response to exogenous stimuli (Zhao et al., 2019; Zhang et al., 2020). For example, transcriptomic studies revealed differential expression of circRNAs in various tissues and developmental stages such as root, stem, leaf, and flowers, as well as in response to pathogens and biotic stresses such as drought, salinity, cold, and nutrient deficiency (Zhang et al., 2020). Plant circRNAs have also been shown to form R-loop to regulate gene expression in Arabidopsis (Conn et al., 2017) and regulate chromatin organization in maize (Liu et al., 2020). Although various studies have proposed that plant circRNAs can act as miRNA sponges, very few experimental evidence is available (Chu et al., 2020).

Plant reproduction is one of the most important stages as its success determines crop yield. The switch from the vegetative to reproductive phase of a plant occurs in response to internal (age) and external signals (photoperiod or temperature), leading to changes in the overall gene expression during reproductive development (Wong et al., 2013; Luo et al., 2021). Studies have identified lncRNAs and circRNAs as the key regulatory elements

during plant reproduction (Yamaguchi e Abe, 2012; Golicz et al., 2018; Zhao et al., 2019) as these are reported to perform critical regulatory roles such as chromatin remodeling, transcription, molecular scaffolding and sequestering proteins and RNAs (Ransohoff et al., 2018; Yu et al., 2019; Budak et al., 2020) (Figure 1).

In this review, we summarize the recent findings on the role of lncRNAs and circRNAs in rice reproductive development. Rice, one of the major staple crops consumed by over half the world's population. Rice is grown in subtropical and tropical areas. Rice is the source of calories and nutrition in many developing countries. Rice production must be increased by 1.5x by 2030 to meet the growing population's demand. Rice crop yield is sensitive to the environment and climate change. Rice improvement through genomic and modern technology is much needed to meet the future demand.

LncRNAs regulate flowering

Flowering starts with transforming shoot apical meristem into inflorescence meristem. The floral organs then originate from the floral meristem that form lateral organs such as carpel, anther, and pollen (Itoh et al., 2005). In Arabidopsis, three lncRNAs termed COLDAIR (cold assisted intronic noncoding RNA), COOLAIR (cold-induced long antisense intragenic RNA), and COLDWRAP (cold of winter-induced noncoding RNA from the promoter) have been shown to play a role in vernalization and floral transition by epigenetically modify the chromatin and silence the repressor FLC (Heo and Sung, 2011; Csorba et al., 2014; Kim and Sung, 2017).

LncRNAs have been shown to regulate flowering and different stages of reproductive development in rice (Table 1, Figure 2). Recently Shin et al. (2022) have reported that OsMADS56-mediated flowering control is strictly regulated by an lncRNA, RIFLA (Rice Flowering Associated), originating from the first intron of the *OsMADS56* gene. *OsMADS56* is a MIKC-type MADS-box protein that acts as a floral repressor. Overexpression of *OsMADS56* in transgenic rice delays the onset of flowering (Ryu et al., 2009). Overexpression of lncRNA, RIFLA inhibited the expression of *OsMADS56* gene but enhanced the expression of flowering inducers genes such as *Hd3a* (Heading date 3a) and *RFT1* (RICE FLOWERING LOCUS T 1), resulting in the early flowering phenotype (Shin et al., 2022).

LncRNAs regulate pollen development and male-fertility

Pollen development within the anther locules requires the expression and regulation of hundreds of genes during which mature fertile pollen is produced (Singh & Bhalla, 2007; Singh et al., 2008) Pollen, a haploid male gametophyte, contains male

germ cells formed from meiocytes (or pollen mother cells) after meiosis, followed by asymmetric mitotic division to give rise to a larger vegetative cell and a smaller generative cell (Haerizadeh et al., 2006; Golicz et al., 2021). Two sperm cells are produced from the generative cell. The transcriptional repertoire of vegetative, generative and sperm cells is quite distinct (2007; Okada et al., 2005; Sharma et al., 2011; Russell et al., 2012). The knowledge of gene regulatory control during these development stages is limited. The involvement of lncRNAs in pollen development has been revealed in some plant species such as *Brassica rapa* (Huang et al., 2018), cotton (Li et al., 2019) and tomato (Lamin-Samu et al., 2022). In rice, systematic identification studies have demonstrated a highly enriched and specific expression of lncRNAs in anthers, pointing to the involvement of lncRNA in pollen development. Anther-specific lncRNAs have been suggested to be involved in germ cell development or meiosis, potentially by acting as competing endogenous RNAs (ceRNAs) to sequester flowering-related miRNAs such as miR160 or miR164 from their target genes (Zhang et al., 2014). Studies in autotetraploid rice have revealed differential expression of 444 lncRNAs during meiosis in the anther and ovary. Some lncRNAs, such as lncRNAs derived from TCONS_00057811, TCONS_00055980 and TCONS_00130461, showed high levels of tissue-specific expression in meiotic stage anthers. Overexpression of TCONS_00057811 (lncRNA57811) reduced pollen fertility and seed setting in transgenic lines compared with wild type (Li et al., 2020).

LncRNAs have been demonstrated to regulate male fertility and pollen development in rice (Table 1). For example, in rice growing under long-day photoperiod conditions, the expression of LDMAR (long-day specific male-fertility-associated RNA), a lncRNA with a length of about 1200 nt, is essential for normal pollen development. However, a single nucleotide mutation altered the secondary structure of LDMAR, which subsequently promoted the methylation of the LDMAR putative promoter and decreased its expression. This reduction in LDMAR expression, which was more observed explicitly during the long-day photoperiod, activated programmed cell death in developing anthers and caused photoperiod-sensitive male sterility (Ding et al., 2012).

LncRNAs could also be involved in fertility transition in rice. Wuxiang S is a rice line that produces a male-sterile phenotype when the temperature is > 24°C and the day length is > 12 hours. However, Wuxiang S can become male-fertile and have normal anthers when plants (with panicle length ~1 cm) are transferred to a growth condition under 12 hours day photoperiod with a temperature of about 21°C. A comparison of RNA sequencing and bioinformatic analysis between the Wuxiang S male-sterile line and its photo-thermo transitioned male-fertile counterpart revealed differential expression of 622 lncRNAs during different stages of pollen development. Functional analysis of cis and trans targets of lncRNAs revealed genes involved in pollen development-related processes, including regulation of carbohydrate metabolism, starch accumulation, lipid metabolism, formation of anther cuticle and

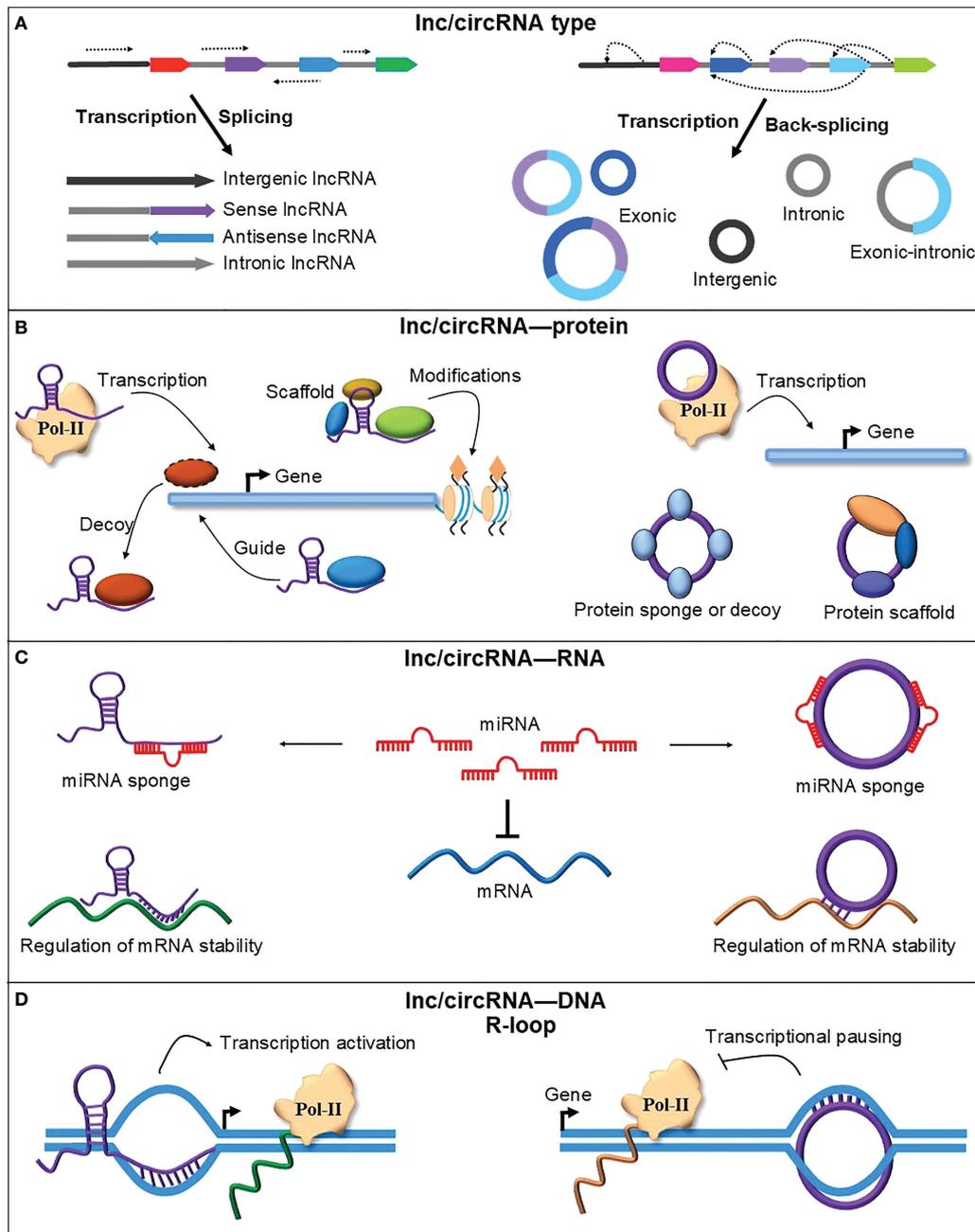


FIGURE 1

A schematic representation of lncRNAs and circRNAs types and their mode of action. (A) RNA polymerase II transcription and canonical splicing produce different types of lncRNAs from genic and intergenic regions. CircRNAs are also transcribed using RNA polymerase II but spliced via an uncanonical type of splicing named backsplicing. CircRNAs are produced from genic and intergenic regions but mainly from the circularization of one or more exons. (B) lncRNAs and circRNAs could interact with different proteins to perform their function. They can interact with RNA Polymerase II (Pol-II) components to regulate transcription. lncRNAs can recruit different proteins, such as transcription factors and chromatin modifiers, to guide them to their place of activity or titrate them away from their site of action to signal the activation or deactivation of gene expression. CircRNA can also sponge or scaffold various proteins to perform their cellular function, such as regulating gene expression, translation, and cell division (Huang et al., 2020). (C) lncRNAs and circRNAs can bind to other RNAs and regulate gene expression. lncRNAs and circRNAs block or reduce the negative effect of miRNAs on target mRNAs by sponging miRNAs. lncRNAs and circRNAs can also modulate the stability and translation of mRNAs by directly binding their target mRNAs on the recognition site of miRNAs or RNA-binding proteins (Sebastian-de-laCruz et al., 2021; Wu et al., 2022). (D) lncRNAs and circRNAs can directly bind DNA and form an RNA-DNA hybrid or R-loop. By forming the R-loops, lncRNAs and circRNAs regulate the transcription of their parent or adjacent genes by affecting the RNA polymerase II transcriptional machinery.

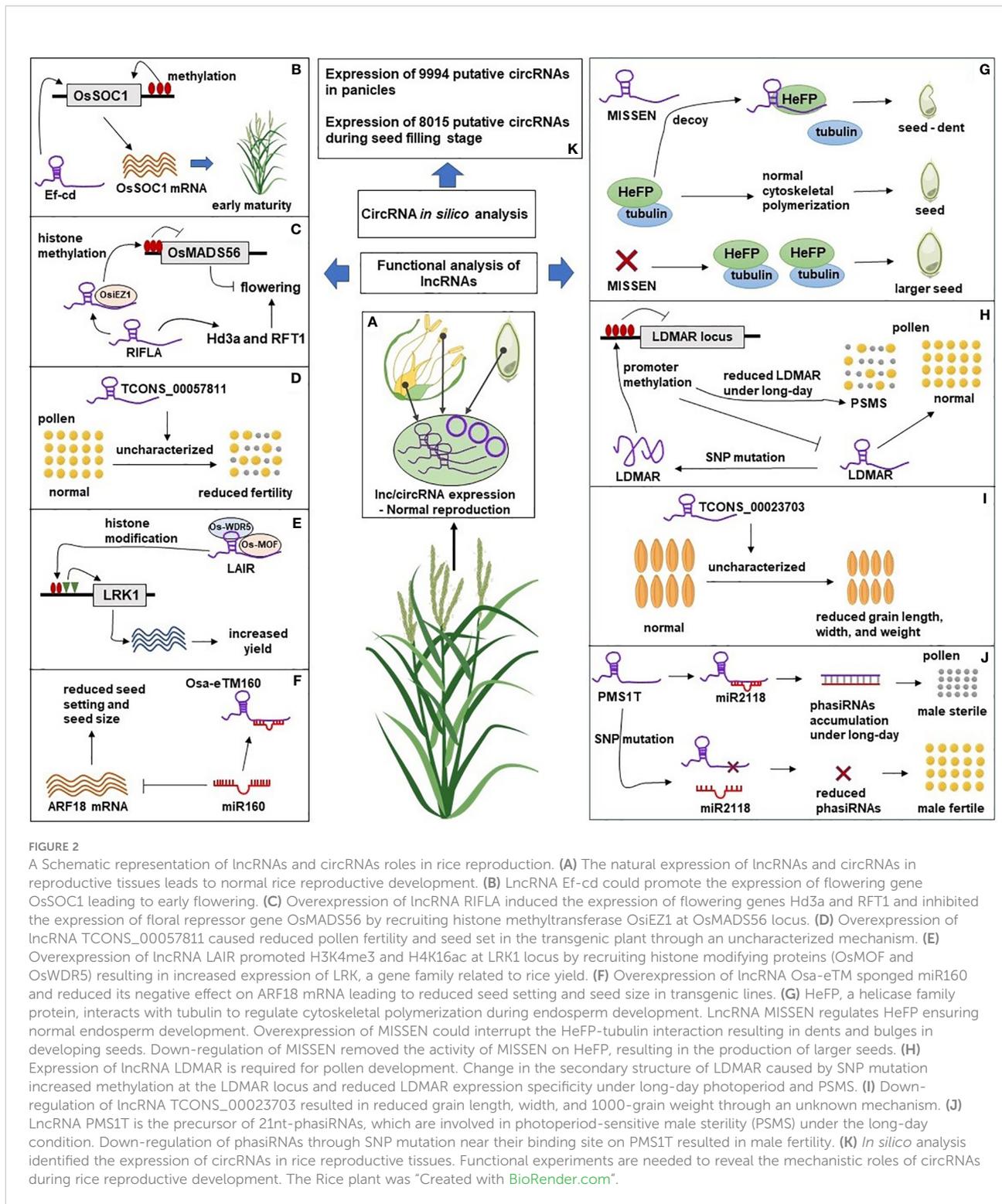
TABLE 1 A list of lncRNAs and circRNAs studied during rice reproduction.

lncRNA name	Transcribed region	Expression specificity	lncRNA function	Mechanism of action	reference
nTCONS_00057811	–	Anther specific expression	Overexpression resulted in reduced pollen fertility and seed set	Uncharacterized	(Li et al., 2020)
RIFLA	The first intron of OsMADS56	Suppresses the expression of the parent gene	Overexpression resulted in early flowering by inhibiting the OsMADS56 gene (floral repressor) and inducing Hd3a and RFT1 genes (floral inducers)	Histone methylation (H3K27me3) by recruiting histone methyltransferase OsiEZ1	(Shin et al., 2022)
LDMAR	Sense strand relative to transcript AK111270	Anther specific expression at vacuolated pollen cell stage required for normal pollen growth and development under long-day photoperiod	Down-regulation of LDMAR activated programmed cell death in developing anthers under long-day photoperiod and caused photoperiod-sensitive male sterility	Altered secondary structure of LDMAR caused by SNP mutation, increased methylation in the promoter region of LDMAR	(Ding et al., 2012)
LAIR	The antisense strand of neighboring region of the LRK cluster gene	High level of expression in three-leaf stage shoot and reproductive tissues	Overexpression positively regulated the expression of many LRK genes and increased seed production	Activation of the LRK1 gene by promoting H3K4me3 and H4K16ac. Binds untranslated regions and histone modifying proteins (OsMOF and OsWDR5) to regulate the epigenetic changes	(Wang et al., 2018)
Osa-eTM160	Intergenic	High and specific expression in the early reproductive stage	Osa-eTM attenuated the repression of osa-miR160 on osa-ARF18 mRNAs through target mimicry manner to affect seed setting and seed size	Targets miR160 to regulate the expression of Osa-ARF18 mRNA during the anther development	(Wang et al., 2017)
MISSEN	Intergenic	Specific expression in reproductive tissues	Overexpression of MISSEN resulted in dents and bulges in the seed. The down-expression of MISSEN resulted in larger seeds by increasing nuclear division and endosperm cellularization	Inhibits the interaction of HeFP (a helicase family protein) with tubulin and causes abnormal cytoskeletal polymerization during endosperm development	(Zhou et al., 2021b)
TCONS_00023703	–	High expression during seed development	RNAi-based knock-down resulted in reduced grain length, width, and 1000-grain weight	Uncharacterized	(Zhao et al., 2020)
Ef-cd	<i>Ef-cd</i> , lncRNA transcribed from the antisense strand of flowering activator <i>OsSOC1</i> gene	High expression in panicles	<i>Ef-cd</i> lncRNA enhanced the expression of <i>OsSOC1</i> , leading to early maturity without affecting the rice yield. <i>Ef-cd</i> improved nitrogen utilization and promoted photosynthesis rate	<i>Ef-cd</i> can potentially promote the level of methylation (H3K36me3) in the <i>OsSOC1</i> locus	(Fang et al., 2019)
PMS1T	<i>Pms1</i> locus encodes lncRNA s	PMS1T has preferential expression in young panicles	The phasiRNAs regulate photoperiod-sensitive male sterility (PSMS) in rice SNP in PMS1T near the miR2118 recognition site changed the accumulation of phasiRNAs and fertility	Functions as a precursor of 21-nt phasiRNAs when targeted by miR2118	(Fan et al., 2016)
Os06circ02797	Intron of <i>Os06g04610</i>	–	Sequesters miR408	Uncharacterized	(Zhou et al., 2021a)
Total of 8015 putative circRNAs	–	Rice grains at filling stage	Some circRNAs could potentially act as miRNA sponges	Uncharacterized	(Chen et al., 2022)
Total of 9994 putative circRNAs	–	Panicles	Some circRNAs could potentially act as miRNA sponges. Gene ontology analysis suggested role of parent gene of circRNAs in various biological processes such as metabolic, developmental, and reproductive processes	Uncharacterized	(Wang et al., 2019)

pollen exine, regulation of rice tapetum degeneration, and hormone signal transduction (Wang et al., 2021).

lncRNAs can also be expressed as a precursor of miRNAs and function during rice pollen development. It has been shown

that over 700 long intergenic non-coding RNAs (lincRNAs) were expressed specifically in inflorescences. These reproductive stage-specific lincRNAs contain a complementary sequence for miR2118 which could cleave through DICER-LIKE4 (DCL4)



protein at the miR2118 site to generate 21-nucleotide phased small interfering RNAs (phasiRNAs) in the germ cells. PhasiRNAs are associated with MEIOSIS ARRESTED AT LEPTOTENE1 (MEL1), which is a rice Argonaute (AGO)

protein that regulates the progression of meiosis and development of germ cells in male and female organs (Komiya et al., 2014). Rice *mel1* mutants show irregular development of germ cells, such as prevention of the chromosome condensation

at the early meiosis and anomalous vacuolation of pollen mother cells (Nonomura et al., 2007). It is proposed that the MEL1-phasiRNAs interactions could modulate target genes involved in maintaining the germ-cell identity and its normal development in the pre-miotic to mitotic stages (Komiya et al., 2014). *PMSIT* transcribed from *Pms1* (photoperiod-sensitive genic male sterility 1) locus is a particular example of lncRNAs that function as a precursor of phasiRNAs when targeted by miR2118. It has been observed that under the long-day condition, *PMSIT* accumulate in the photoperiod-sensitive male sterility lines, and a single SNP in *PMSIT* nearby the miR2118 recognition site can alter fertility through changing phasiRNAs accumulation (Fan et al., 2016).

LncRNAs regulate ovule development and seed production

Ovules are female reproductive organs with distinct gene expressions that, after fertilization, develop into seeds (Shi and Yang, 2011). In rice, differential expression of lncRNAs has been observed between female-sterile and female-fertile rice during different stages of ovule development, suggesting the role of lncRNAs in ovule development and abortion of female gametophyte (Liu et al., 2019). lncRNA XLOC_057324, with high expression in young panicles and pistils, has also been suggested to play a role in flower development and sexual reproduction. Mutant rice lines with a T-DNA insertion in XLOC_057324 showed an early flowering phenotype with a reduced fertility rate (Zhang et al., 2006; Zhang et al., 2014). Early flowering rice cultivars generally have lower seed yields than late flowering cultivars because of the shorter maturity duration. Studies have demonstrated that the innate variation in *Ef-cd* (early flowering-completely dominant) gene can decrease the maturity duration without affecting the rice yield. *Ef-cd* is an antisense lncRNA overlapping the *Os-SOC1* gene, and this lncRNA can enhance the expression of the *Os-SOC1* gene. Further analysis revealed that *Ef-cd* improves the yield in early flowering rice by promoting nitrogen utilization and photosynthesis (Fang et al., 2019).

The long non-coding RNAs also regulate seed development in rice. lncRNA MISSEN (mis-shapen endosperm), known previously as XLOC_057324, has been demonstrated to inhibit HeFP (a helicase family protein) from interaction with tubulin during endosperm development causing abnormal cytoskeletal polymerization. Overexpression of MISSEN suppressed normal development of endosperm, resulting in dents and bulges in the seed, while lines with reduced expression of MISSEN showed increased nuclear division and endosperm cellularization resulting in larger seeds compared with wild type. It is worth noting that histone methylation inhibits MISSEN expression after pollination. (Zhou et al., 2021b). lncRNAs also regulate seed development through lncRNA-miRNA-mRNA

interactions. lncRNA *Osa-eTM160* (eTM: endogenous target mimic) has been shown to regulate the expression of *Osa-ARF18* mRNAs by targeting *Osa-miR160*. *Osa-ARF18* mRNAs and *Osa-miR160* have high expression in early anther developmental stages. Overexpression of *Osa-eTM160* reduced the activity of *Osa-miR160* and caused a reduced seed setting rate and seed size in transgenic lines (Wang et al., 2017). Driving epigenetic changes is another way that lncRNAs regulate seed development in rice. The involvement of lncRNA LAIR (leucine-rich repeat receptor kinase antisense intergenic RNA) transcribed from neighboring regions of the LRK (leucine-rich repeat receptor kinase) cluster gene has been demonstrated during seed development. Overexpression of LAIR could positively regulate the expression of many LRK genes leading to increased seed production. Further, it was revealed that LAIR could bind 5' and 3' untranslated regions of the LRK1 gene and histone modification proteins such as Os-MOF and Os-WDR5. LAIR then activates the LRK1 gene by promoting H3K4me3 and H4K16ac modifications (Wang et al., 2018).

Differential expression of lncRNAs and alternative splicing have also been observed during seed development in rice (Kiegle et al., 2018; Zhao et al., 2020). For instance, RNA sequencing studies on developing seeds (three and seven days after pollination) revealed 482 lncRNAs with differential expression patterns. Transgenic rice lines with RNAi-based downregulation of expression of lncRNA TCONS_00023703 showed a significant reduction in grain length, width, and 1000-grain weight (Zhao et al., 2020). In addition, more exon inclusion in lncRNAs has been observed in embryo; a such example is LOC9270896 which potentially produces 20 variant transcripts with a length between 3,714 to 4,616 bp, but the predominate variant in the embryo was a short variant (593 bp) that all three introns were spliced out (Kiegle et al., 2018).

CircRNAs are involved in reproductive development

Genome-wide RNA expression analysis has revealed that circRNAs show preferential expression in different plant tissues. For example, of 5372 identified circRNAs in soybean, 2647, 1644, and 484 circRNAs were expressed preferentially in the root, stem, and leaf tissues, respectively, and the remaining circRNAs were common between two or three tissues (Zhao et al., 2017). Similar results have been found when circRNA expression was compared between root, leaf, and flower tissues in Arabidopsis (Philips et al., 2020). A comprehensive survey of rice transcriptome identified 15,122 lncRNAs and 7902 circRNAs in root, leaf and panicle tissues (Zhou et al., 2021a). Both lncRNAs and circRNAs are expressed in a highly tissue-specific manner, with panicle-specific expression being the most pronounced. Moreover, the tissue-specific expression of circRNAs was much higher compared to lncRNAs. GO enrichment for parental genes of circRNAs revealed the

involvement of circRNAs in reproductive and post-embryonic development in a panicle.

Further, circRNA Os06circ02797 generated by locus Os06g04610 harbors binding sites for OsmiRNA-408. OsmiRNA408 positively enhances photosynthesis and regulates grain yield in rice increasing panicle branches and grain number (Zhang et al., 2017). Zhou et al. (2021a) produced CRISPR-Cas9 edited stable transgenic rice lines with deleted Os06circ02797 locus. The seedlings of Os06circ02797 null mutant demonstrated rapid growth phenotype following seed germination. Further analysis revealed the functioning of circRNA-miRNA-mRNA regulatory network where Os06circ02797 binds and sequesters OsmiRNA408.

The circular RNAs are also involved in pollen development. For example, in *Brassica rapa*, differential expression of circRNAs during pollen development has been observed. Functional analysis suggested their potential roles in pollen-related developmental processes such as cell cycle, meiosis/mitotic cell division, and polysaccharide biosynthesis (Babaei et al., 2021). In rice, circRNAs were found to be involved in pollen development and fertility transition in photo-thermosensitive genic male sterile lines. Transcriptome comparison of young panicles from male sterile and fertile lines at different developmental stages detected specific expression patterns of circRNAs during pollen development and fertility transition. Functional annotation analysis suggested that circRNAs could have important roles in the regulation of cell differentiation, cell division, regulation of hormone levels, response to temperature stimulus, and floral organ development. CircRNAs could also act as ceRNAs by targeting miR399, an ambient temperature-responsive flowering regulator (Teotia and Tang, 2015; Wang et al., 2019).

CircRNAs are also reported to be involved in grain filling in rice. For instance, in a recent study, over 8000 putative circRNAs were identified during different stages of seed development. *In silico* analysis suggested that while some circRNAs could act as miRNA decoys targeting miR-164 and miR-398, other circRNAs could function in various processes such as carbohydrate metabolic processes, embryo development, and lipid transport (Chen et al., 2022).

Concluding remarks

Reproduction, a critical developmental process, determines yield and productivity of crop plants. Transcriptome studies

using next-generation sequencing experiments have revealed the differential expression pattern of lncRNAs and circRNAs and their wide distribution during reproductive processes in rice. Although the importance and diverse potential functions of lncRNAs and circRNAs have been proposed using *in silico* analysis, the molecular function of only a few reproductive-related lncRNAs has been elucidated to date. The involvement of lncRNAs in flowering, pollen development, fertility, seed development, and seed yield add another layer of complexity to plant gene regulation during growth and development. However, the journey toward understanding the role of lncRNAs and circRNAs in plant reproduction has just begun. We expect more functional studies unraveling reproductive processes to be published in the coming years.

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All authors listed have made a substantial, direct, and intellectual contribution to the work, and approved it for publication.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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