Plant non-coding RNAs and epigenetics

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Epigenetics plays a large role in various aspects of plant biology, including development, response to biotic and abiotic stresses, silencing of transposable elements, and maintenance of genome stability. In plants, epigenetic regulation involves histone and DNA modifications and non-coding RNAs including small RNAs (sRNAs) and long non-coding RNAs (lncRNAs). This issue of *Science China Life Sciences* includes five review articles and eight research articles that explore functions and mechanisms of different types of sRNAs and lncRNAs, histone modification, and DNA methylation.

NON-CODING RNAs: THE LONG AND THE SHORT OF THEM

MicroRNAs (miRNAs) are a class of endogenous sRNAs that are processed from hairpin-structured precursors. miRNA expression often exhibits spatial and temporal specificity. Xu et al. present an expression atlas of *Arabidopsis* miRNAs by sequencing sRNA libraries generated from 27 different organ/tissue types (Xu et al., 2018). They found that different miRNA members within the same family have distinct spatial and temporal expression patterns and some miRNAs are produced from different arms of their hairpin

precursors at different developmental stages. This work provides a rich resource for future investigation of miRNA functions in *Arabidopsis*. A subset of miRNAs has been identified to target the transcripts encoding plant resistance (R) proteins, the immune receptors that recognize pathogen effectors and trigger rapid defense responses. Li summarizes the recent progress in our understanding of how plant miRNAs reduce R gene levels under normal conditions and allow induction of R gene expression under stress conditions (Deng Y. et al., 2018).

Phased siRNAs (phasiRNAs) are generated from long RNA precursors (transcripts from protein-coding or non-coding genes) targeted by miRNAs at intervals of 21 or 24 nt in plants. Interestingly, grass phasiRNAs are specifically expressed in reproductive organs. Yu et al. summarize current knowledge on phasiRNAs in male germ cells and their possible biological functions and mechanisms in anther development and male fertility (Yu et al., 2018). Transfer RNA-derived small RNAs (tsRNAs) are generated from precursor or mature tRNAs. Zhu et al. review the recent progress in the discovery, biogenesis, and function of tsRNAs in higher plants (Zhu et al., 2018).

In addition to sRNAs, lncRNAs play critical roles in plant development and environmental acclimation. Deng et al. systematically analyze lncRNAs in five monocot and five dicot species (Deng P. et al., 2018). They found that the majority of lncRNAs have high sequence conservation at the intra-species and sub-species levels, similar to mRNAs. In-

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triguingly, they demonstrate that although highly diverged at the nucleotide level, some lncRNAs are conserved by position in the genome at the inter-species level and they are often co-expressed with their adjacent protein-coding genes. Wang et al. show that a lncRNA, named *HID1* (hidden treasure 1), acts as a negative regulator of cotyledon greening in addition to its role in photomorphogenesis (Wang et al., 2018). *HID1* acts downstream of phytochrome-interacting factors 3 (PIF3) during the dark-to-light transition. Genetic ablation of *HID1* resulted in the elevated transcript levels of the protochlorophyllide oxidoreductases known to catalyze Pchl_{ide} to chlorophyllide conversion, and subsequently leading to an increased greening rate of etiolated seedlings. Lariat-derived circular RNAs (laciRNAs) are produced during pre-mRNA splicing. They are previously thought as by-products of mRNA processing in higher eukaryotes. Cheng et al. identify an *Arabidopsis* laciRNA that plays an essential role in gene regulation and plant development, suggesting that the production of laciRNAs may have biological significance (Cheng J. et al., 2018).

RNA editing is a type of post-transcriptional modification that includes nucleotide insertion/deletion or conversion. In higher plants, RNA editing usually occurs in plastids and mitochondria and plays important roles in organelle biogenesis, environmental adaptation and development. Yan et al. discuss the divergent roles of the plant RNA editing factors such as pentatricopeptide repeat (PPR) proteins, multiple organelle RNA editing factors (MORE, also known as RIP), organelle RNA recognition motif (ORRM) containing proteins, protoporphyrinogen IX oxidase 1 (PPO1) and organelle zinc finger 1 (OZ1) (Yan et al., 2018).

HISTONE AND DNA MODIFICATIONS: AN EVER-GROWING PUZZLE

In eukaryotes, epigenetic inheritance is mainly established by histone modification and DNA methylation. The covalent modifications on histone can be “read” by specific protein domains and subsequently trigger downstream signaling events. Liu et al. review recent structural studies on the recognition of the epigenetic marks on histones by reader proteins, and summarize the general and unique features of histone mark readers in plants (Liu et al., 2018).

EARLY FLOWERING IN SHORT DAYS (EFS, also known as SDG8) is the major contributor for H3K36 methylation in *Arabidopsis* (Kim et al., 2005; Zhao et al., 2005). Cheng et al. uncover a novel function of *EFS/SDG8* in embryogenesis (Cheng L. et al., 2018). They found that the mutation in *EFS/SDG8* causes large embryo and altered histone modification at an imprinted gene called *MOP9.5*. Lin et al. show that overexpression of the mutated forms of histone H3 (H3.1K36M and H3.3K36M) causes serious

developmental defects (Lin et al., 2018). The H3K36M mutation inhibits the activity of *EFS/SDG8* and changes the modifications of endogenous histone H3, including acetylation at lysine 9 (H3K9ac), trimethylation at lysine 27 (H3K27me3), di- and tri-methylation at lysine 36 (H3K36me2 and H3K36me3).

The SU(VAR)-3-9-related protein family member SUVR2 is involved in transcriptional gene silencing in both RNA-dependent and -independent pathways (Thorstensen et al., 2006). Luo et al. demonstrate that SUVR2 is mono-sumoylated in *planta* (Luo et al., 2018). The sumoylation of SUVR2 is required for the interaction of SUVR2 with the chromatin-remodeling proteins CHR19, CHR27, and CHR28 and transcriptional gene silencing.

In addition to histone modification, DNA methylation plays a vital role in gene expression and plant development. Chen et al. performed genome-wide profiling of DNA methylation at single-base resolution by whole-genome bisulfite sequencing in tomatoes (Chen et al., 2018). Taking the advantage of the tomato epimutant *colourless non-ripening* (*Cnr*) and virus-induced gene silencing (VIGS) technology, they found that two genes, named *SIDET1* and *SIPDS*, are involved in the pigmentation in *Cnr* fruits.

These review and research articles underscore the importance of epigenetic mechanisms that regulate a variety of biological processes in plants. Our understanding of the functions and mechanisms of chromatin modifications and noncoding RNAs is still very limited. Further efforts and resources are needed to solve these ever-growing puzzles.

Compliance and ethics The author(s) declare that they have no conflict of interest.

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Biographical Sketch

Dr. Jia-Wei Wang was born in Shanghai and graduated from the Department of Life Science and Technology, Shanghai Jiao Tong University in 1999. He received a Ph.D. degree at Shanghai Institutes for Biological Sciences, Chinese Academy of Sciences (CAS) in 2005. He went to Germany as a postdoc in 2005 and received postdoctoral training at Max Planck Institute for Developmental Biology. His independent research began from 2011 and he is currently a principal investigator at National Key Laboratory of Plant Molecular Genetics (NKLPMG), CAS Center for Excellence in Molecular Plant Sciences, Institute of Plant Physiology and Ecology (SIPPE), CAS. The main research focus of his group is plant life cycle and developmental timing.

Dr. Yijun Qi is a Professor in School of Life Sciences and Center for Plant Biology at Tsinghua University in Beijing. He completed a Ph.D. in plant virology at Zhejiang University. He is an expert on RNA silencing in plants. Work in his laboratory includes investigating the functions of small RNAs and long non-coding RNAs, biochemical and molecular analysis of Argonaute complexes, and RNA-directed repair of DNA double-strand breaks.