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REVIEW

Epigenetics in the modern era of crop improvements

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Epigenetic mechanisms are integral to plant growth, development, and adaptation to environmental stimuli. Over the past two decades, our comprehension of these complex regulatory processes has expanded remarkably, producing a substantial body of knowledge on both locus-specific mechanisms and genome-wide regulatory patterns. Studies initially grounded in the model plant Arabidopsis have been broadened to encompass a diverse array of crop species, revealing the multifaceted roles of epigenetics in physiological and agronomic traits. With recent technological advancements, epigenetic regulations at the single-cell level and at the large-scale population level are emerging as new focuses. This review offers an in-depth synthesis of the diverse epigenetic regulations, detailing the catalytic machinery and regulatory functions. It delves into the intricate interplay among various epigenetic elements and their collective influence on the modulation of crop traits. Furthermore, it examines recent breakthroughs in technologies for epigenetic modifications and their integration into strategies for crop improvement. The review underscores the transformative potential of epigenetic strategies in bolstering crop performance, advocating for the development of efficient tools to fully exploit the agricultural benefits of epigenetic insights.

epigenetics | plant development | plant immunity | crop improvement | stress responses

Introduction

Epigenetic regulation is crucial for living organisms from growth and development to environmental adaptations. With the rapid development of technologies and methodologies, the investigations of epigenetic regulation have been capacitated from single locus to genome wide scale. This leads to an explosive understanding of the importance of non-coding intergenic regions and silenced heterochromatin. Novel epigenetic modifications at DNA, RNA, and histone levels and regulatory mechanisms involving non-coding RNAs and chromatin architectural changes have also been uncovered and intensively studied. Importantly, new sequencing technologies enabled in-depth studies of agricultural and horticultural plants, as well as comparative evaluations from a population level, leading to an increasing awareness of epigenetic regulations in key agronomic traits. Here we present a comprehensive review on plant epigenetics, covering basic molecular mechanisms revealed mainly from model plant Arabidopsis to their roles in physiological processes and agronomic traits in agriculturally important plants, including rice, wheat, soybean, and tomatoes. We further discuss recent advances in technologies developed for epigenetic modifications and crop improvement. We conclude with a discussion on the perspectives for the efficient application of epigenetic strategies in crop improvement.

DNA methylation

General features of DNA methylation

DNA methylation is a conserved epigenetic mark in mammals and plants. It functions in transposable element (TE) silencing and gene regulation, and is therefore important for the maintenance of genome integrity and the regulation of plant development (Law and Jacobsen, 2010; Zhang et al., 2018b). In plants, DNA methylation occurs in different sequence contexts, including CG, CHG, and CHH (where H = A, T, or C), the levels of which vary considerably across plant species, from as low as 5.4% (CG), 2.6% (CHG), and 2.5% (CHH) in *Chlamydomonas reinhardtii* to as high as 92.6% (CG), 81.2% (CHG), and 18.9% (CHH) in *Beta vulgaris* (Cokus et al., 2008; Niederhuth et al., 2016). Besides, DNA methylation tends to be differentially enriched in different cell types or tissues (Bartels et al., 2018; Kawakatsu et al., 2016; Walker et al., 2018), which also appears as a widely conserved phenomenon across flowering plants (Xu et al., 2022; Zemach et al., 2010; Zhang et al., 2022a).

Establishment and maintenance of DNA methylation

A great body of knowledge has been obtained through Arabidopsis studies, showing that *de novo* DNA methylation is established through the RNA-directed DNA Methylation (RdDM) pathway. This pathway consists of the DNA-dependent RNA

polymerase IV (Pol IV)-mediated "triggering step" and the Pol V-mediated "targeting step" (Du et al., 2022; Huang et al., 2021b; Zhai et al., 2015a). Besides the two plant-specific RNA polymerases, the key components of the RdDM pathway also include RNA-DEPENDENT RNA POLYMERASE 2 (RDR2), DICER-LIKE 3 (DCL3), ARGONAUTE 4 (AGO4), AGO6, AGO9, DOMAIN REARRANGED METHYLTRANSFERASE 2 (DRM2), CLASSY1-4, SAWADEE HOMEODOMAIN HOMOLOGUE 1 (SHH1), SUPPRESSOR OF VARIEGATION 3-9 HOMOLOG PROTEIN 2 (SUVH2), SUVH9, DEFECTIVE IN RNA DIRECTED DNA METHYLATION 1 (DRD1), DEFECTIVE IN MERISTEM SILENCING 3 (DMS3) and RNA-DIRECTED DNA METHYLATION 1 (RDM1) (Johnson et al., 2014; Law et al., 2013; Sigman et al., 2021; Wang et al., 2023a; Wang et al., 2022e; Wongpalee et al., 2019; Xie et al., 2023a; Yang et al., 2018a; Zhong et al., 2012; Zhou et al., 2018a). Recent studies have also highlighted the role of the microrchidia (MORC) family ATPases in facilitating the RdDM pathway (Li et al., 2023d; Xue et al., 2021b).

In Arabidopsis, CG cytosine methylation is maintained by METHYLTRANSFERASE 1 (MET1), which is proposed to be recruited to hemi-methylated DNA by VARIANT IN METHYLATION (VIM) proteins. This model is reminiscent of the function of mammalian DNA methyltransferase 1 (DNMT1) and UHRF1 (ubiquitin-like with PHD and RING finger domains 1) (Bostick et al., 2007; Sharif et al., 2007; Woo et al., 2008; Woo et al., 2007; Zhang et al., 2018b).

In Arabidopsis, most CHG methylation is maintained by CHROMOMETHYLASE 3 (CMT3), and the positive feedback loop involves H3K9 methyltransferase KRYPTONITE (KYP, also known as SUVH4), along with its homologs SUVH5 and SUVH6 (Lindroth et al., 2001; Stroud et al., 2014). Mechanistically, SUVH4/5/6 bind to methylated DNA to catalyze H3K9me2, and H3K9me2 is recognized by the DNA methyltransferases CMT2 and CMT3, which then catalyze DNA methylation (Du et al., 2012). A similar mechanism has also been implicated in maize (Du et al., 2012; Stoddard et al., 2019).

In regions where RdDM activity is suppressed, such as the H1-containing heterochromatin, CHH methylation is mainly maintained by CMT2. Since CMT2 can also be recruited through the recognition of the H3K9me2 histone modification, which in turn is affected by CMT3-dependent CHG methylation, the maintenance of asymmetric CHH methylation may also be affected by CMT3 (Stroud et al., 2014).

DNA demethylation

Demethylation of DNA can occur via two primary pathways: passive demethylation and active demethylation (Zhang et al., 2022a). Passive demethylation occurs when the activity of DNA methyltransferases is inhibited during DNA replication, resulting in a dilution of methylation marks (Zhang et al., 2018b). One example is the transcriptional repression of *MET1*, *CMT3*, and *KYP* by the DREAM complex, which consists of DIMERIZATION PARTNER, RETINOBLASTOMA-LIKE PROTEIN, E2F, and MULTIVULVAL B CORE (Ning et al., 2020).

In contrast, active demethylation is catalyzed by DNA glycosylases and apurinic/apyrimidinic lyases, which include REPRESSOR OF SILENCING 1 (ROS1), DEMETER (DME), DEMETER-LIKE 2 (DML2), and DML3 (Du et al., 2023; Zhang et al., 2022a). For efficient demethylation at certain genomic loci, the involvement of the INCREASED DNA METHYLATION (IDM) complex and the SWI2/SNF2-Related 1 (SWR1) chromatin remodeling complex are also essential (Duan et al., 2017a; Nie et al., 2019). Additionally, the expression of ROS1 is positively regulated by the level of DNA methylation within its promoter (Liu et al., 2021a; Xiao et al., 2019; Zhang et al., 2022a).

DNA methylation readers

In plants, DNA methylation is recognized by proteins containing either the methyl-CpG binding domain (MBD) or the SET- and RING-ASSOCIATED (SRA) domain. These proteins function in various DNA methylation-related pathways, including DNA methylation or demethylation, histone modification, transcriptional activation or silencing, etc. Specifically, the Arabidopsis genome encodes thirteen MBD proteins, among which MBD2, MBD5, MBD6, and MBD7 are known to bind to symmetrically methylated DNA (Ichino et al., 2021; Springer and Kaeppler, 2005; Wang et al., 2024b; Zemach and Grafi, 2003). These MBD proteins play crucial roles in gene silencing or participating in the DNA demethylation process (Boone et al., 2023; Feng et al., 2021; Ichino et al., 2021; Ichino et al., 2022; Lang et al., 2015; Potok et al., 2019; Preuss et al., 2008; Ren et al., 2024; Sijacic et al., 2019; Wang et al., 2015; Wang et al., 2024b).

In Arabidopsis, SRA domains are found in both VIM and SUVH family proteins. VIM1–3 possibly bind to hemi-methylated CG sites and further recruit MET1 to maintain CG DNA methylation (Woo et al., 2008; Woo et al., 2007). SUVH1 and SUVH3 counteract the silencing effects of DNA methylation by recruiting DNAJ transcriptional activators (Harris et al., 2018; Li et al., 2016; Li et al., 2018a; Nie et al., 2019; Xiao et al., 2019; Zhao et al., 2019a). SUVH4–6 recognize CHG DNA methylation and catalyze the H3K9me2 modification, forming a positive feedback loop with CMT3 (Du et al., 2014; Ebbs and Bender, 2006; Jackson et al., 2002; Li et al., 2018a). SUVH2 and SUVH9 recognize methylated DNA and recruit Pol V and MORC6 to reinforce the silencing effect of the RdDM pathway (Jing et al., 2016; Johnson et al., 2014; Liu et al., 2014c).

Histone modifications and variants

H3K27me3

H3K27me3, a repressive histone mark predominantly found in euchromatic regions, is pivotal in orchestrating plant development and responses to environmental stimuli (Kakutani et al., 2011; Kim et al., 2021; Wang et al., 2024c; Wu et al., 2020; Xiao and Wagner, 2015; Zhang et al., 2007). H3K27me3 can be added by the evolutionarily conserved Polycomb repressive complex 2 (PRC2) and erased by a group of Jumonji (JMJ) domain-containing histone demethylases, including JMJ11, JMJ12, JMJ13, JMJ30, and JMJ32 (Crevillén et al., 2014; Gan et al., 2014; Lu et al., 2011; Margueron and Reinberg, 2011; Zheng et al., 2019b).

PRC2 can be recruited to certain chromatin regions by transcription factors (TFs) that recognize Polycomb response elements (PREs), leading to cell type-, tissue type- or developmental stage-specific deposition of H3K27me3 (Kim et al., 2022; Xiao et al., 2017a; Zhou et al., 2018b). This process is exemplified by the core components of PRC2: EMBRYONIC FLOWER2 (EMF2), which regulates reproductive growth (Yoshida et al., 2001); VERNALIZATION2 (VRN2), involved in

vernalization (Helliwell et al., 2006); and FERTILIZATION-INDEPENDENT SEED2 (FIS2), which impacts seed development (Hennig et al., 2005).

Conversely, JMJ histone demethylases dynamically demethylate H3K27me3, alleviating transcriptional repression during plant adaptation to environmental challenges, such as heat stress responses (He et al., 2021; He et al., 2022; Liu et al., 2019b; Yamaguchi et al., 2021). A recent study has highlighted the interaction between nuclear-localized α-ketoglutarate dehydrogenase (KGDH) and various JMJ proteins, which inhibits their demethylase activity and thus modulates genome-wide gene expression under light conditions (Huang et al., 2023). Both JMJ proteins and the PRC2 complex are integral to cell fate determination, including the development of stomata cells and male germline cells (Kim et al., 2022; Zhu et al., 2023).

H3K9me2

Di- or tri-methylation of histone H3 lysine 9 (H3K9me2 and H3K9me3) is a hallmark of constitutive heterochromatin across eukaryotes (Grewal, 2023). In somatic tissues, H3K9me2 is typically mutually exclusive with the facultative heterochromatin mark H3K27me3. However, these two marks can coexist at certain loci in Arabidopsis pollen vegetative cells and endosperm (Moreno-Romero et al., 2019; Zhu et al., 2023), highlighting the tissue specificity in defining heterochromatin.

In Arabidopsis, three SUVH methyltransferases, SUVH4–6, are responsible for catalyzing H3K9me2 at pericentromeric regions (Hu and Du, 2022). Different SUVH proteins exhibit distinct binding preferences towards DNA methylation of different sequence contexts (Li et al., 2018a; Zhang et al., 2023d). The removal of H3K9me2 is catalyzed by the H3K9me2 demethylase, INCREASE IN BONSAI METHYLATION 1 (IBM1) (Inagaki et al., 2010). The loss-of-function mutant of IBM1 exhibits ectopic H3K9me2 accumulation and transcriptional silencing, which is also accompanied by the removal of activating histone modifications (Inagaki et al., 2017; Oya et al., 2022). Additionally, DNA Topoisomerase VI acts to prevent the spreading of H3K9me2 at pericentromeric regions (Méteignier et al., 2022).

The H3K9me2 readers include Agenet domain-containing protein1 (ADCP1 or AGDP1), and AGDP3, which function in heterochromatin silencing and gene anti-silencing, respectively (Zhang et al., 2018a; Zhao et al., 2019b; Zhou et al., 2022).

H3K4me3

In eukaryotes, H3K4me3 is a conserved "activating" histone modification predominantly located near the transcription start sites (TSS) of actively transcribed genes (Howe et al., 2017). The current working model suggests that H3K4me3 methyltransferases interact with the serine 5 phosphorylated C-terminal domain of RNA polymerase II (CTD-Ser5P), which further leads to co-transcriptional deposition of H3K4me3 (Ding et al., 2011b; Fromm and Avramova, 2014; Ng et al., 2003).

In *Saccharomyces cerevisiae*, the Set1 methyltransferase, a component of the COMPASS (Complex Proteins Associated with Set1) complex, is responsible for mono-, di-, and trimethylation at histone H3 lysine 4 (H3K4me1/2/3) (Briggs et al., 2001; Miller et al., 2001; Ng et al., 2003; Roguev et al., 2001). The Arabidopsis genome encodes five Trithorax (ATX1 to ATX5) and seven Trithorax-related (ATXR1 to ATXR7) proteins (Alvarez-Venegas and Avramova, 2002; Baumbusch et al., 2001). ATX1 has been shown to exhibit histone H3K4 methyltransferase activity in plants (Alvarez-Venegas and Avramova, 2002).

H3K36me3

H3K36me3 represents another type of "activating" histone modification, which is deposited by the enzyme Set2 in yeast and SETD2 in humans (McDaniel and Strahl, 2017; Strahl et al., 2002). Set2 interacts with the serine 2 phosphorylated C-terminal domain of RNA polymerase II (CTD-Ser2P) and predominantly deposits H3K36me3 towards the 3′ ends of genes, which highlights its function in transcription elongation (Li et al., 2003; Xiao et al., 2003). In Arabidopsis, the homologs of yeast Set2 include SDG4, SDG7, SDG8, and SDG26 (Cartagena et al., 2008; Ji et al., 2024; Xu et al., 2008; Zhao et al., 2005). Levels of both H3K36me2 and H3K36me3 modifications are significantly diminished in *sdg8* mutants, but not in *sdg26* mutants (Xu et al., 2008). SDG8 contains a CW domain and exhibits a binding preference for H3K4me1, establishing a direct link between H3K4 and H3K36 modifications (Liu and Huang, 2018).

Histone acetylation

Histone acetylation (HAc) weakens the interaction between histones and DNA by neutralizing the positive charge of histones, thereby promoting transcription (Allis and Jenuwein, 2016). HAc occurs on over 40 different lysine residues across all four core histones (Shvedunova and Akhtar, 2022). The dynamic regulation of gene expression by HAc involves its "writing" by histone acetyltransferases (HATs) (Brownell et al., 1996), "reading" by bromodomain-containing proteins (Dhalluin et al., 1999), and "erasing" by histone deacetylases (HDACs) (Allis and Jenuwein, 2016; Taunton et al., 1996). In addition, both HATs and HDACs also exhibit enzymatic activities toward non-histone proteins (Chen et al., 2017; Shvedunova and Akhtar, 2022).

Histone deacetylation, mediated by HDACs, plays a critical role in numerous biological processes (Chen et al., 2020; Cui et al., 2023; Xiong et al., 2022). Recent research underscores the importance of histone deacetylation in the accumulation of other repressive epigenetic modifications (Qüesta et al., 2016; Yang et al., 2022a; Zeng et al., 2020), the establishment of heterochromatin (Qüesta et al., 2016; Watts et al., 2018; Żylicz et al., 2019), and transcriptional silencing (Earley et al., 2006; Hristova et al., 2015; Yang et al., 2020b).

The bromodomain is a conserved protein module present in HAc "reader" proteins in both animals and plants. In Arabidopsis, BROMODOMAIN-CONTAINING PROTEIN1 (BRD1), BRD2, and BRD13 are critical components of the SWI/SNF (switch defective/sucrose nonfermentable) chromatin remodeling complex (Jarończyk et al., 2021; Yu et al., 2021c). MBD9 is another example of a bromodomain containing protein, and a SWR1 complex component, which functions in the deposition of H2A.Z and DNA demethylation (Nie et al., 2019; Potok et al., 2019; Sijacic et al., 2019).

Histone variants

The core nucleosome is an octameric complex containing two molecules each of the H2A, H2B, H3, and H4 histones. During

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DNA replication, these histones are integrated into the newly synthesized chromatin, and can be subsequently replaced by different histone variants to confer distinct regulatory features.

In plants, there are three commonly observed H3 histone variants: the replication-dependent H3.1, the replacement variant H3.3, and the centromeric H3 (CenH3). H3.1 is enriched in heterochromatin, while H3.3 is enriched in euchromatin (Stroud et al., 2012). The differential assembly and enrichment of H3.1 and H3.3 in various chromatin regions are influenced by their sequence variations at positions 87 and 90 (serine 87 and alanine 90 in H3.1; histidine 87 and leucine 90 in H3.3) (Shi et al., 2011). Additionally, the plant-specific phenylalanine residue at position 41 of H3.1 is also important for its genome-wide distribution (Lu et al., 2018). In addition to H3.1 and H3.3, other plant H3 variants include H3.10 and H3.15, which are found in sperm and wounded tissues, respectively.

H2A variants, namely H2A.Z, H2A.X, and the plant-specific H2A.W, exhibit distinct characteristics. In actively transcribed genes, H2A.Z predominantly occupies the +1 nucleosome, while H2A and H2A.X are spread throughout the entire gene body (Lei and Berger, 2020). Notably, H2A.Z is also abundant in the gene bodies of transcriptionally repressed genes and facultative heterochromatin (Lei and Berger, 2020; Talbert and Henikoff, 2014). In contrast, H2A.W is present in constitutive heterochromatin and transposons but is absent in genes. The incorporation of H2A.W relies on the chromatin remodeler DECREASE IN DNA METHYLATION 1 (DDM1) and aids in heterochromatin condensation (Osakabe et al., 2021; Yelagandula et al., 2014). Additionally, H2A.X plays a role in DNA damage repair (Lorković and Berger, 2017; Waterworth et al., 2019). Consequently, the distribution pattern of H2A variants distinguishes genes from transposons and is linked with their transcriptional activities in varying ways.

H2B variants exhibit significant diversity and lineage-specific characteristics in plants (Jiang et al., 2020). Within the Arabidopsis genome, there are 11 genes encoding H2B, which can be categorized into three classes based on sequence conservation. The majority of H2B genes show elevated expression in organs undergoing active cell division, while H2B.3 is preferentially expressed in mature tissues, suggesting its function as a replacement variant (Jiang et al., 2020). Notably, H2B.7/8/10 are predominantly found in pollen, with H2B.8 potentially playing a role in chromatin compaction within sperm cells through phase separation (Buttress et al., 2022).

Histone H1 originates from bacteria, and exists in three forms in Arabidopsis (Kasinsky et al., 2001). H1.1 and H1.2 exhibit ubiquitous and stable expression, while H1.3 is induced by stresses, suggesting a potential role as a replacement variant (Jerzmanowski et al., 2000).

Histone variants also influence plant biological processes through variant-associated modifications (Borg et al., 2021). For instance, both H3.10 and H3.15 are characterized by the absence of H3K27me3 modifications, a possible mechanism of H3K27me3 reprogramming during gametogenesis and cell dedifferentiation (Borg et al., 2020; Yan et al., 2020). The maintenance of heterochromatin depends on H3.1K27me1 modification mediated by ATXR5/6, which is inhibited by serine 31 in H3.3 (Dong et al., 2021; Jacob et al., 2014). Moreover, H3.1 is essential for the inheritance of H3K27me3 during cell division (Jiang and Berger, 2017). The diverse functions of H2A.Z in gene expression may also involve its modifications. Acetylated H2A.Z is localized around the TSS of actively transcribed genes (Crevillén et al., 2019), while monoubiquitylated H2A.Z is deposited along the body of transcriptionally repressed genes (Gómez-Zambrano et al., 2019). DNA damage repair relies on the phosphorylation of the SQ motif of H2A.X and H2A.W.7 in euchromatin and heterochromatin, respectively (Lorković et al., 2017; Turinetto and Giachino, 2015).

Chromatin remodeling

In Arabidopsis, major types of chromatin remodelers include SWI/SNF, ISWI (imitation switch), INO80 (inositol requiring 80), SWR1, and CHD (chromodomain helicase DNA-binding) (Clapier and Cairns, 2009). Except for CHD, all other chromatin remodelers exist as multi-subunit complexes, whereas the Arabidopsis CHD3 chromatin remodeler, PICKLE, mainly exits as a monomer. ISWI and CHD remodelers promote nucleosome assembly and sliding, SWI/SNF enhances chromatin accessibility by evicting nucleosomes, SWR1 replaces the canonical histone H2A with its variant, H2A.Z, while INO80 catalyzes the reciprocal reaction (Clapier et al., 2017). These chromatin remodelers play essential roles in various biological processes, including transcription, DNA replication, DNA damage repair, and DNA methylation (Han et al., 2015; Shang and He, 2022).

The composition and function of chromatin-remodeling complexes

The Arabidopsis ISWI chromatin remodelers consist of two redundant core subunits, CHROMATIN REMODELING 11 (CHR11) and CHR17, along with DDT domain-containing accessory proteins (Dong et al., 2013). Through proteomics assays, three types of ISWI complexes were identified, including CRAF (CHR11/17-RLT1/2-ARID5-FHA2), CDM (CHR11/17-DDP1/2/3-MSI3), and CDD (CHR11/17-DDR/W) (Gu et al., 2020; Shang and He, 2022; Tan et al., 2020). Similar to other eukaryotes, the ISWI complex in plants regulates nucleosome spacing, which in turn influences the transcription of specific genes and TEs (Li et al., 2014a; Zhang et al., 2023e).

In Arabidopsis, there are three classes of SWI/SNF chromatin remodelers, which include the BRAHMA (BRM) containing BAS-type, the SPLAYED (SYD) containing SAS-type, and the MINUSCULE1/2 (MINU1/2) containing MAS-type (Diego-Martin et al., 2022; Fu et al., 2023b; Guo et al., 2022a; Han et al., 2015; Jarończyk et al., 2021; Lei et al., 2024; Yu et al., 2021c; Yu et al., 2020). BAS and SAS bind to numerous common target genes, while MAS primarily binds to a distinct set of target genes (Fu et al., 2023b; Guo et al., 2022a). Although all three SWI/SNF complexes facilitate chromatin accessibility near TSS, SAS mainly acts at distal promoter and upstream intergenic regions (Fu et al., 2023b; Guo et al., 2022a).

The INO80/SWR chromatin remodelers, which include SWR1 and INO80, are characterized by a conserved split ATPase domain (Clapier and Cairns, 2009). In Arabidopsis, the SWR1 chromatin remodeler, known as PHOTOPERIOD-INDEPENDENT EARLY FLOWERING1 (PIE1), is responsible for the replacement of H2A with H2A.Z, a process critical for the regulation of gene transcription. Other interacting components of the Arabidopsis SWR1 complex include TRA1A/B, MBD9, as well as the ISWI chromatin remodelers CHR11/17 (Gómez-Zambrano et al., 2018; Luo et al., 2020c; Nie et al., 2019; Potok et al., 2019;

Sijacic et al., 2019). Both TRA1A/B and MBD9 are essential for maintaining the genome-wide levels of H2A.Z (Luo et al., 2020c; Potok et al., 2019; Sijacic et al., 2019), whereas CHR11/17 couple H2A.Z deposition with nucleosome positioning (Luo et al., 2020c).

The Arabidopsis INO80 complex comprises three modules: the ATPase module, the helicase-SANT-associated (HSA) module, and the N-terminal domain (NTD) module (Shang et al., 2021). Studies have indicated the role of the Arabidopsis INO80 complex in both H2A.Z eviction and deposition (Willige et al., 2021; Xue et al., 2021a; Yang et al., 2020a). Notably, the INO80 NTD module contains plant-specific accessory subunits and interacts with the COMPASS complex, mediating histone H3K4me3 modification (Shang et al., 2021). Arabidopsis INO80 has been shown to regulate various biological processes, including flowering transition, thermo-morphogenesis, ethylene signaling, and DNA damage repair (Shang and He, 2022; Xue et al., 2021a).

Functional interplay between chromatin remodelers, histone modifications, histone variants and histone chaperones

The proper functions of chromatin remodelers depend on their target specific recruitment on chromatin. One prevalent recruiting mechanism is through direct or indirect recognition of specific histone modifications or DNA motifs (Gómez-Zambrano et al., 2018; Nie et al., 2019; Tan et al., 2020). For example, Arabidopsis BAS-type SWI/SNF complexes can recognize histone acetylation through their subunits BRD1, BRD2, and BRD13 (Yu et al., 2021c). In addition, since certain chromatin remodeler components exhibit differential binding preference towards specific histone variants (Gu et al., 2020), histone variants also influence the enrichments and function of chromatin remodelers at specific chromatin loci (Corcoran et al., 2022; Kang et al., 2019). For example, FORKHEAD-ASSOCIATED DOMAIN 2 (FHA2), an ISWI subunit, demonstrates a strong preference for binding to the H2A.Z/H2B histone dimer, but not to the H2A/H2B dimer (Gu et al., 2020).

Histone chaperones also exert a profound influence on the process of chromatin remodeling (Du et al., 2020; Michl-Holzinger et al., 2022; Zhong et al., 2022). Histone chaperones can be classified based on the types of histone variants they interact with (Avvakumov et al., 2011). Specifically, the H2A-H2B histone chaperones include FAcilitates Chromatin Transcription (FACT), Nucleosome Assembly Protein 1 (NAP1), NAP1-Related Protein 1 (NRP1), and Chaperone for H2A.Z-H2B 1 (Chz1) (Du et al., 2020; Luo et al., 2020a; Wang et al., 2020c; Wu et al., 2023). The H3-H4 histone chaperones include Anti-Silencing Factor 1 (ASF1) and histone regulator A (HIRA). It has been shown that AtChz1A/B promote the deposition of H2A.Z in chromatin by interacting with the SWR1 complex subunit, ACTIN-RELATED PROTEIN 6 (ARP6) (Wu et al., 2023). Similarly, ASF1 collaborates with HIRA, playing a pivotal role in the deposition of the H3.3-H4 histone variants in eukaryotic organisms. These examples underscore the importance of chaperone partnerships in ensuring the correct assembly of nucleosomes (Zhong et al., 2022).

Alternatively, chromatin remodelers can also be recruited to chromatin by interacting with sequence-specific transcription factors (Liang et al., 2022; Richter et al., 2019; Shu et al., 2022; Willige et al., 2021; Xue et al., 2021a; Zhang et al., 2023a; Zhu et al., 2024). For instance, the recruitment of BRM to *SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1 (SOC1)* is facilitated by the GNC (GATA, NITRATE-INDUCIBLE, CARBON METABOLISM INVOLVED) transcription factor (Yang et al., 2022c). The involvement of transcription factor in chromatin remodeling also explains mechanistically how plants regulate gene expression to cope with diverse environmental signals. For example, under shade conditions, PHYTOCHROME-INTERACTING FACTOR 7 (PIF7) recruits the ASF1-HIRA complex to shade-responsive genes, mediating the deposition of H3.3 (Yang et al., 2023a).

Upon the genomic recruitments, chromatin remodelers are also capable of modulating, either directly or indirectly, both histone modifications and gene transcription (Hu et al., 2022a; Li et al., 2022c; Yang et al., 2020b). For example, recent studies have reported that the chromatin recruitment of INO80 complex is associated with both EARLY FLOWERING 7 (ELF7) and COMPASS-like modules, which contribute to the regulation of transcription elongation and histone modification (Xue et al., 2021a; Zhao et al., 2023a).

Organization of 3D chromatin

Chromosomes occupy specific regions in the nucleus instead of being randomly distributed during interphase in eukaryotes. This structured organization, known as the chromosome territory, has been observed through both fluorescence *in situ* hybridization (FISH) and high-throughput chromosome conformation capture (Hi-C) experiments (Bintu et al., 2018; Cremer and Cremer, 2001; Lieberman-Aiden et al., 2009; Stevens et al., 2017). Based on the relative positioning of centromeres and telomeres post-folding, both the "Rosette" and "Rabl" conformation have been reported for different plant species (Dong and Jiang, 1998; Oko et al., 2020; Tiang et al., 2012). Although the chromosome territory may undergo dynamic changes under certain conditions (de Lima et al., 2022; Ginno et al., 2018; Parada et al., 2004; Zhu and Wang, 2019), whether such changes will lead to phenotypic consequences remains to be determined (Wang et al., 2023f).

In a nucleus, different chromosome regions are found to be partitioned into two epigenetically distinct groups, namely A/B compartments, forming a distinct "plaid" pattern in the Hi-C interaction map (Dong et al., 2017; Grob et al., 2014; Liao et al., 2022; Liu et al., 2017; Pei et al., 2022; Wang et al., 2021a; Wang et al., 2018). The A compartments are associated with activating chromatin features, including higher levels of gene density, transcriptional activity, chromatin accessibility, and active histone marks. To the contrary, the B compartments exhibit the opposite characteristics (Bi et al., 2017; Dong et al., 2017; Feng et al., 2014; Lieberman-Aiden et al., 2009; Wang et al., 2022c; Wang et al., 2018; Yin et al., 2023; Zhang et al., 2019b). Switches between A/B compartments are usually associated with changes in gene transcriptional activities (Li et al., 2024b; Ni et al., 2023; Pei et al., 2022; Wang et al., 2021b).

Topologically associating domains (TADs) and TAD-like structures are megabase-sized contact domains found across many species, including plants (Crane et al., 2015; Dixon et al., 2012; Hsieh et al., 2015; Li et al., 2024b; Nora et al., 2012; Phillips-Cremins et al., 2013; Sexton et al., 2012; Sun et al., 2024a; Yin et al., 2023). Within each TAD are multiple chromatin loops that define the interactions between different genes and their regulatory regions. Two specific types of loops

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have been reported. While loops formed between the 5′ and 3′ ends of a gene were found to enhance gene transcription by facilitating efficient use of RNA Polymerase II (Cavalli and Misteli, 2013; Larkin et al., 2012; Tan-Wong et al., 2008), genic loops within the gene body, excluding the promoter region, are presumed to impede gene expression by blocking the recruitment of RNA Polymerase II (Dong et al., 2018; Guo et al., 2018b). Moreover, loops may bring into the contact of *cis*-regulatory elements and specific epigenetic modifications, consequently influencing the transcriptional activity (Ariel et al., 2014; Dong et al., 2017; Krivega and Dean, 2012; Louwers et al., 2009; Pontvianne and Liu, 2020; Sun et al., 2024a).

One key question in the field is the causal relationship between chromosome 3D structures and other biological processes occurred on chromatin, such as DNA and histone modifications and gene transcription. Studies have shown that changes in DNA methylation lead to compartment switches, and also affect TAD boundary formation and loop formation, but have minimal impacts on the relative territories occupied by different chromosomes (Feng et al., 2014; Gagliardi and Manavella, 2020; Rowley et al., 2017; Wang et al., 2022b; Zhang et al., 2023f). The importance of H3K27me3 and H2AK121ub in loop formation has also been demonstrated in Arabidopsis (Huang et al., 2021c; Yin et al., 2023).

Small RNA

Small RNA (sRNA) mediates gene and TE silencing in a sequence-specific manner. Based on their biogenesis and functional modes, plant small RNAs can be mainly categorized into microRNAs (miRNAs), phased small interfering RNAs (phasiRNAs), and heterochromatic siRNA (hc-siRNA). While plant miRNAs and phasiRNAs mainly regulate gene expression at the post-transcriptional level (PTGS) (Axtell, 2013; Vaucheret and Voinnet, 2024), plant hc-siRNAs mainly regulate gene expression at transcriptional level (TGS) and are extensively studied for their role in guiding DNA methylation through the RdDM pathway (Yu et al., 2019). This chapter primarily describes the noncanonical roles of miRNAs and phasiRNAs in TGS.

miRNAs

miRNAs are defined by the precise excision of the small RNA duplex from the stem of a hairpin-like precursor RNA (Axtell and Meyers, 2018). Plant genomes typically encode hundreds of *MIRNA* (*MIR*) genes, many of which exist in families and are deeply conserved across the plant kingdom (Cuperus et al., 2011; Nozawa et al., 2012). Plant miRNAs regulate gene expression mainly through target slicing, which requires a high degree of complementarity between miRNA and its target mRNAs (Liu et al., 2014b). Key protein factors of miRNA biogenesis include the RNase III endonuclease DCL1 and RNA methyltransferase HEN1 (Park et al., 2002; Reinhart et al., 2002; Yu et al., 2005). The mature miRNAs are assembled onto AGO effector proteins to form miRNA-induced silencing complexes (miRISCs) (Baumberger and Baulcombe, 2005; Fang and Qi, 2016; Mi et al., 2008).

Apart from their canonical roles in PTGS, miRNAs are increasingly implicated in epigenetic regulation. Several Arabidopsis epigenetic modifier genes, including *CMT3*, *DRM2*, *SUVH5/6*, and *INVOLVED IN DE NOVO 2 (IDN2)*, are miRNA targets (Bennett et al., 2022; Jha and Shankar, 2014; Papareddy et al., 2021). Besides, some miRNAs or secondary siRNAs triggered by miRNAs have been shown to direct DNA methylation through a mechanism akin to RdDM (Bao et al., 2004; Chen et al., 2011; Khraiwesh et al., 2010; Wu et al., 2012; Wu et al., 2010). In addition, miRNAs initiate the biogenesis of "epigenetically activated" siRNAs (easiRNAs) by targeting and cleaving transposon transcripts, which further mediate interploidy hybridization barriers by monitoring chromosome dosage in developing seeds (Borges et al., 2018; Creasey et al., 2014; Martinez et al., 2018). Interestingly, in both animals and plants, certain miRNAs and AGO protein are found to be associated with chromatin and promote transcription (Liu et al., 2018a; Liu et al., 2018b; Xiao et al., 2017b; Yang et al., 2019).

PhasiRNAs

The term "phased" describes the "head-to-tail arrangement" in small RNA production following miRNA-mediated cleavage of the primary precursors, which can occur via either a "one-hit" or "two-hit" mode (Allen et al., 2005; Axtell et al., 2006; Fei et al., 2013; Liu et al., 2020; Montgomery et al., 2008; Vazquez et al., 2004; Xia et al., 2017). PhasiRNAs function in diverse plant biological processes, including disease resistance and reproductive development (Fan et al., 2016; Johnson et al., 2009; Shivaprasad et al., 2012a; Teng et al., 2020; Xia et al., 2015; Zhai et al., 2011; Zhai et al., 2015b). Studies in both Arabidopsis and maize have suggested that phasiRNAs also contribute to DNA methylation in *cis* at their own loci (Wu et al., 2012; Zhang et al., 2021a). For example, elevated levels of DNA methylation, primarily in the CHH context, have been observed at maize phasiRNAs producing loci (PHAS), which also depend on the action of 24-nt phasiRNAs (Dukowic-Schulze et al., 2016; Zhang et al., 2021a).

RNA modification and processing

N^6-methyladenosine methyltransferase

Over 170 types of post-transcriptional RNA modifications have been identified in all kingdoms of life. Among them, N^6-methyladenosine (m^6A) is the most abundant mRNA modification in eukaryotes, and the first RNA modification found in plants (Jia et al., 2011). In the following sections, we summarize the cellular processes of writing, erasing, and reading of m^6A modifications, which are carried out by m^6A methyltransferases, m^6A demethylases, and m^6A binding proteins, respectively. The functions of m^6A modifications in regulating plant agronomic traits are also discussed.

So far, two types of m^6A methyltransferases have been characterized in Arabidopsis. In one type, the m^6A methyltransferase complex is composed of MTA (plant ortholog of human METTL3), MTB (plant ortholog of human METTL14), and FKBP12 INTERACTING PROTEIN 37KD (FIP37, an ortholog of human WTAP), along with accessory proteins, including VIRILIZER (VIR), HAKAI, and HAKAI-interacting zinc finger protein (HIZ2) (Růžička et al., 2017; Shen et al., 2016; Song et al., 2024; Zhang et al., 2022b; Zhong et al., 2008). Loss of function of MTA, MTB, or FIP37 leads to embryo lethality in Arabidopsis (Bodi et al., 2012; Shen et al., 2016; Zhong et al., 2008). Conditional complementation of MTA or FIP37 during the embryonic state results in severe defects in apical dominance,

organ specification, and shoot meristem development (Bodi et al., 2012; Shen et al., 2016). In rice, OsFIP37-ASSOCIATED PROTEIN 1 (OsFAP1) recruits the m^{6}A writer subunit OsFIP37 to install m^{6}A on *OsYUCCA3* transcript during male meiosis (Cheng et al., 2022). *OsFIP37* deficiency causes early degeneration of microspores and abnormal meiosis (Zhang et al., 2019a). Knockdown of *MTA* or *MTB* delays fruit ripening of strawberry (Zhou et al., 2021a).

In addition to the MTA-MTB m^{6}A methyltransferase complex, FIONA1, an ortholog of human METTL16, serves as another m^{6}A methyltransferase for U6 small nuclear RNA (snRNA) and a small subset of mRNAs. Deficiency in FIONA1 leads to early flowering and hypocotyl elongation under continuous red and far-red light (Wang et al., 2022a). It has also been shown that blue light receptor CRYPTOCHROME 2 (CRY2) and SUPPRESSOR of PHYTOCHROME A (SPA1) activate the RNA methyltransferase activity of FIONA1 to regulate chlorophyll homeostasis in response to blue light (Jiang et al., 2023). Furthermore, CRY2 also interacts with MTA, MTB, and FIP37 to install m^{6}A on transcripts of core circadian clock genes (Wang et al., 2021e). These discoveries suggest that both types of m^{6}A methyltransferases function cooperatively downstream of the blue light receptor to regulate plant light responses.

N^6-methyladenosine demethylase

Mammals contain two Fe(II)/α-KG-dependent mRNA m^{6}A demethylases, FTO (fat mass and obesity associated gene) and ALKBH5 (AlkB homologs 5). Although plants lack FTO orthologs, recent studies have demonstrated the potential application of human FTO in crop breeding, where overexpression of human FTO boosts field yield of rice and potato, and increases gene editing efficiency in soybeans. This enhancement is attributed to FTO-mediated m^{6}A demethylation, which induces chromatin openness (Bai et al., 2024; Yu et al., 2021a).

ALKBH9B and ALKBH10B, the Arabidopsis orthologs of ALKBH5, have been characterized as functional m^{6}A demethylase (Duan et al., 2017b; Jia et al., 2011; Zheng et al., 2013). ALKBH9B specifically removes m^{6}A from the genomic RNA of Alfalfa mosaic virus (AMV), and positively regulates viral systemic invasion in plants (Martínez-Pérez et al., 2017). Therefore, ALKBH9B serves as a potential target in obtaining virus resistant crops. ALKBH10B regulates the m^{6}A demethylation and the transcript stability of flowering regulator genes, such as *FT*, *SPL3*, and *SPL9*. Deficiency in ALKBH10B leads to late flowering phenotype (Duan et al., 2017b). Both ALKBH9B and ALKBH10B regulate abscisic acid (ABA) responses in Arabidopsis (Tang et al., 2021; Tang et al., 2022). In tomatoes, the m^{6}A demethylase SlALKBH2 removes the m^{6}A modification from the transcripts of *SlDML2*, a DNA demethylase, and is required for the stabilization of *SlDML2* transcripts and normal fruit ripening (Zhou et al., 2019). OsALKBH9 is an m^{6}A demethylase in rice, and is required for male fertility. The null mutation in *OsALKBH9* leads to defective tapetal programmed cell death (PCD) and excessive accumulation of microspore exine (Tang et al., 2024).

N^6-methyladenosine reader

In addition to m^{6}A writers and erasers, five human YTH-domain family proteins have been characterized as m^{6}A readers. The Arabidopsis and rice genome each encodes 13 and 12 YTH-domain proteins, respectively, suggesting the redundancy and complexity of plant m^{6}A readers (Ao et al., 2023; Cai et al., 2023; Guo et al., 2022b). Supporting this notion, the Arabidopsis YTH domain proteins, EVOLUTIONARILY CONSERVED C-TERMINAL REGION 2 (ECT2), ECT3, and ECT4 function redundantly to regulate leaf morphogenesis and the ABA responses (Arribas-Hernández et al., 2018; Arribas-Hernández et al., 2020; Scutenaire et al., 2018; Song et al., 2023). Other plant traits regulated by ECTs include trichome branching, and responses to bacterial infection and abiotic stresses (Cai et al., 2024; Lee et al., 2024; Wei et al., 2018; Wu et al., 2024).

ECTs function to regulate mRNA stabilities and translation efficiency in association with RNA processing proteins, such as poly(A) binding protein 2 (PAB2), PAB4, and the decapping protein, decapping 5 (DCP5) (Cai et al., 2024; Song et al., 2023). These regulatory activities of RNAs were found to occur in specific stress related subcellular organelles and/or phase-separated condensates (Lee et al., 2024; Wu et al., 2024). For example, ECT1 sequesters SA-induced m^{6}A-modified mRNAs for degradation in cytosolic ECT1 condensates that colocalize with processing bodies (P-bodies) and stress granules (SGs) in response to bacterial infection (Lee et al., 2024).

In addition, the long isoform of CLEAVAGE AND POLYADENYLATION SPECIFICITY FACTOR 30 (CPSF30-L), which controls the choice of polyadenylation sites, is a plant-specific m^{6}A reader. Disruption of CPSF30-L leads to late flowering, ABA hypersensitivity, and abnormal nitrate metabolism (Hou et al., 2021; Song et al., 2021). FLOWERING LOCUS K (FLK), which contains K-homology (KH) motifs, has been characterized as a new type of m^{6}A reader. It reduces the stability and alters the splicing of *FLOWERING LOCUS C* (*FLC*) to regulate the floral transition (Amara et al., 2023). The RNA binding protein EARLY HEADING DATE6 (EHD6) directly interacts with the m^{6}A reader YTH07, enhancing its m^{6}A binding ability. EHD6 recruits YTH07 and sequesters m^{6}A-modified *CONSTANS-like 4* (*OsCOL4*) transcripts into phase-separated condense (RNP granule), thereby inhibiting protein translation and promoting rice flowering (Cui et al., 2024).

RNA 5-methylcytosine

RNA 5-methylcytosine (m^{5}C) modification is another prevalent mark found across various types of RNAs, including mRNAs, tRNAs, rRNAs, and other non-coding RNAs (Gao and Fang, 2021; Xue et al., 2022). In plants, m^{5}C is mainly enriched within the coding sequences (Cui et al., 2017; David et al., 2017; Tang et al., 2020). In humans, RNA m^{5}C methyltransferases (RCMTs) are primarily composed of the NOL1/NOP2/SUN domain (NSUN) family proteins (Trixl and Lusser, 2019; Yang et al., 2017b). The plant homologs of human NSUN proteins have also been identified, such as OsNSUN2 in rice and AtTRM4B in Arabidopsis (Amort et al., 2017; Cui et al., 2017; Tang et al., 2020). Defects in plant m^{5}C methyltransferases lead to developmental defects of root apical meristems and chloroplasts (Cui et al., 2017; David et al., 2017; Tang et al., 2020).

In addition to RNA m^{5}C writers, m^{5}C demethylases such as Tet methylcytosine dioxygenase 2 (TET2) and ALKBH1, and m^{5}C reader proteins such as Aly/REF export factor (ALYREF) have also been studied in animals (Kawarada et al., 2017; Li et al., 2023c; Wang et al., 2023c; Yang et al., 2017b; Zhang et al., 2020). While homologs of *ALYREF* have been found in the plant

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genomes, their exact functions have not yet been confirmed. Furthermore, a number of RNA m^5C-related protein regulators, such as the fragile X mental retardation protein (FMRP), Y box protein 2 (YBX2), YTH domain-containing family protein 2 (YTHDF2), and Serine/arginine-rich splicing factor 2 (SRSF2) were found to play crucial roles in a spectrum of biological processes in animals, including DNA damage repair, liquid-liquid phase separation (LLPS), and pre-rRNA processing (Dai et al., 2020; Ma et al., 2023; Wang et al., 2022d; Yang et al., 2022b). However, the protein homologs of these novel RNA m^5C regulators and their functional importance in plants remained to be characterized.

In addition to m^6A and m^5C, other RNA modifications found in plants include N^4-acetylcytosine (ac^4C), pseudouridylation (ψ), N^1-methyladenosine (m^1A), and Nicotinamide adenine diphosphate (NAD^+) 5′ end capping. While the precise functions of these diverse RNA modifications are not yet fully understood, studies have implicated their regulatory roles in a broad spectrum of plant biological processes, including chloroplast rRNA maturation, leaf development, seed germination, photosynthesis, ABA signaling, and stress responses (Chen and Witte, 2020; Pan et al., 2020; Wang et al., 2022f; Yang et al., 2020c; Yu et al., 2021b). The transcriptomic distribution patterns (Sun et al., 2019), writers (Xiao et al., 2023), erasers (Pan et al., 2020; Yu et al., 2021b), and readers of these different RNA modifications, as well as their regulatory mechanisms are also under investigation (Li et al., 2023a; Pan et al., 2020; Wang et al., 2023d; Wang et al., 2019; Yu et al., 2021b; Zhang et al., 2019c).

Regulation and modification of RNA poly(A) tails

The poly(A) tail is co-transcriptionally added to the 3′ end of precursor RNA, representing a pivotal element in mRNA quality control and translation efficiency (Passmore and Coller, 2022; Weill et al., 2012). Recent advancements in sequencing methods have significantly improved the measurement of poly(A) tail length. These methods can be mainly grouped into the short-read sequencing platforms-based methods, including TAIL-seq (Chang et al., 2014), mTAIL-seq (Lim et al., 2016), PAL-seq (Subtelny et al., 2014), PAT-seq (Harrison et al., 2015), Poly(A)-seq (Zhao et al., 2019c) and TED-seq (Woo et al., 2018), and the long-read sequencing platform-based methods such as FLAM-seq (Legnini et al., 2019), PAIso-seq (Liu et al., 2019c), FLEP-seq (Jia et al., 2020a; Long et al., 2021b), FLEP-seq2 (Jia et al., 2022), and Nanopore direct RNA sequencing (DRS) (Parker et al., 2020; Wang et al., 2024a). PAL-seq, for instance, has provided insights, revealing that the poly(A) tail length in Arabidopsis leaves is longer than that in yeast but shorter than that in mammalian cells (Subtelny et al., 2014). The median poly(A) tail length in various tissues of Arabidopsis and different plant species ranges from 50 to 100 nt (Jia et al., 2022; Parker et al., 2020; Subtelny et al., 2014). Notably, chloroplast and mitochondrial transcripts have shorter poly(A) tails than nuclear transcripts, with a median length of 13 nt in chloroplasts and 20 nt in mitochondria (Parker et al., 2020). The distribution of poly(A) tail length exhibited distinct phase peaks and tissue-specific patterns in plants, with most Arabidopsis tissues peaking around ~20 and ~45 nt, which is the footprint of one or two cytoplasmic poly(A) binding proteins (PABPC) (Jia et al., 2022). mRNA with the most prolonged half-lives exhibited poly(A) tail length peak at ~45 nt, while the short-lived mRNA had few tails in the corresponding range (Jia et al., 2022). Poly(A) tails in the nucleus displayed longer tail lengths than those in the cytoplasm (Jia et al., 2022), implying the rapid shortening of poly(A) tails before mRNA stabilization in the cytoplasm. ONT-DRS of *ddm1* and *ccr4a ddm1* revealed that the poly(A) tail length of transposon transcripts also showed ~25 nt internal peaks and CCR4a was responsible for TE RNA stability (Wang et al., 2024a). Additionally, the lengths of poly(A) tails in orthologous genes remained relatively consistent among various plant species, highlighting the evolutionarily conserved nature of poly(A) tail length (Jia et al., 2022).

Beyond poly(A) tail length, the presence of non-adenosine residues within poly(A) tails is widespread in Arabidopsis (Jia et al., 2022; Scheer et al., 2021; Zhao et al., 2019c; Zuber et al., 2016). Poly(A)-seq has revealed the presence of guanine in poly (A) tails, showing a negative correlation with the PABP binding efficiency in Arabidopsis genes (Zhao et al., 2019c). Both TAIL-seq and PacBio-sequenced FLEP-seq2 libraries have revealed that uridylation exhibits the highest frequency among all non-A nucleotides, with a predominant occurrence in transcripts featuring a poly(A) tail length of less than 20 nt (Jia et al., 2022; Zuber et al., 2016). RNA uridylation was significantly decreased in the *urt1*, indicating that URT1 functions as the main terminal uridylyltransferases for uridylation (Sement et al., 2013; Zuber et al., 2016). 3′-truncated transcripts were accumulated in the *urt1*, as revealed by 3′ RACE, and transcripts with short poly(A) tails were also accumulated in the *urt1*, as shown by Nanopore direct RNA sequencing. Both findings suggest that uridylation inhibited the 3′ trimming of oligo(A)-tailed mRNAs (Scheer et al., 2021; Sement et al., 2013). In line with this, *in vitro* biochemical experiments demonstrated that uridylation delayed deadenylation (Zuber et al., 2016). Furthermore, LC-MS/MS analysis has revealed that URT1 is associated with several translational repressors and decapping factors (Scheer et al., 2021), indicating that uridylation promotes mRNA degradation. These studies have significantly expanded our understanding of poly(A) tail length dynamics and its biological function in plants.

Epigenetic regulation of plant agronomic traits

Gametophyte development

Plant germline cells are differentiated from somatic cells, during which a subepidermal cell differentiates into megaspore mother cells (MMC) in the ovule and pollen mother cells (PMCs) in the anther. Both local and large-scale chromatin epigenetic reprogramming of histone modifications and DNA methylation occurs during germline cell development, and is critical for plant reproduction (She and Baroux, 2015; She et al., 2013; Yang et al., 2023d).

MMC specification requires precise regulation of DNA methylation (Hernández-Lagana et al., 2016; Mendes et al., 2020; Olmedo-Monfil et al., 2010; Qin et al., 2014; Zhao et al., 2018). The level of CHH methylation (mCHH) is barely detectable at the early MMC stage and gradually increases later during female sporogenesis (Figure 1) (Ingouff et al., 2017). Mutations in the RdDM components may lead to the formation of multiple MMCs within an ovule (Hernández-Lagana et al., 2016; Olmedo-Monfil et al., 2010). The mature female gametophyte contains two

gametes: a haploid egg cell and a diploid central cell. Within the central cell, the enrichment of mCG at genes and TEs is relatively low due to the preferential expression of *DME* before fertilization (Park et al., 2016; Schoft et al., 2011). In contrast, the level of mCHG in the central cell is similar to that in the embryo, and the mCHH level is higher (Figure 1) (Park et al., 2016). In rice, it has been found that small RNAs migrate from the central cell into the egg cell to guide *de novo* DNA methylation (Erdmann et al., 2017; Ibarra et al., 2012). Similar mechanisms may also exist in Arabidopsis.

During Arabidopsis male gametophyte development, meiocytes that originate from PMCs are enveloped by the protective nursery tapetum. The tapetum generates 24-nt siRNAs, which are likely transported into the meiocytes through plasmodesmata, guiding the male sexual-lineage-specific DNA methylation (Long et al., 2021a; Walker et al., 2018; Zhou et al., 2018a). Consequently, meiocytes, microspores, and sperm all exhibit high levels of mCG and mCHG (Figure 1). However, mCHH levels are low in these cells, possibly due to a genome-wide erasure of mCHH during meiocyte differentiation (Calarco et al., 2012; Walker et al., 2018). In contrast, the vegetative cell displays lower levels of mCG and mCHG, as well as more decondensed chromatin (Figure 1) (Jullien et al., 2012; Walker et al., 2018). The loss of DNA methylation at TEs and DNA repeats in the vegetative cell facilitates the production of 24-nt siRNAs (Calarco et al., 2012; Schoft et al., 2011). These siRNAs are then transported into sperm cells to direct DNA methylation (Figure 1) (Calarco et al., 2012; Martínez et al., 2016). Thus, the role of companion cell-derived small RNAs in shaping the epigenetic landscape of reproductive cells may be a conserved feature of both male and female gametogenesis.

Interestingly, there is an overall high level of mCHH but a low level of mCHG DNA methylation in rice sperm cells (Liu et al., 2023b; Zhou et al., 2021b), which differs from the near complete loss of mCHH observed in Arabidopsis sperm cells. These changes in DNA methylation likely begin in the rice meristem long before germ cell differentiation (Higo et al., 2020), and also depend on DNA demethylase (Kim et al., 2019; Liu et al., 2018d; Zhou et al., 2021b).

Histone modifications are also reprogrammed during male gametogenesis. Male germlines exhibit a reduced level of H3K27me3 (Borg et al., 2020; Zhu et al., 2023), likely due to the combined effects of reduced PRC2 activity, increased H3K27me3 demethylation activity, and the incorporation of H3.10, a histone H3 variant that is resilient to H3K27me3 (Borg et al., 2020). However, the loss of H3.10 does not affect the overall H3K27me3 pattern in male gametes and does not cause visible defects in male gametogenesis (Borg et al., 2020; Okada et al., 2005; Zhu et al., 2023). One prominent feature of sperm chromatin is the widespread presence of H3K27me3 and H3K4me3 bivalency (Zhu et al., 2023). Whether this bivalency results from cell heterogeneity or co-exists within a single cell remains to be further characterized.

Fertilization and seed development

During double fertilization, one sperm fuses with the egg cell to produce the embryo, and the other fertilizes the central cell to produce the endosperm. Similar as in animals, upon fertilization, the zygote transcriptome is dominated by maternally inherited transcripts, including small RNA carried over from the egg cell (Anderson et al., 2017; Li et al., 2022a; Liu et al., 2023b). Meanwhile, zygotic genome activation (ZGA) occurs before the first embryonic division, which is characterized by a widespread redistribution of 24-nt sRNAs and a reconfiguration of the paternal DNA methylation to match the maternal methylation pattern (Anderson et al., 2017; Liu et al., 2023b). A continuous increase in the level of mCHH has been observed during the Arabidopsis early embryogenesis and seed development (Figure 1) (Bouyer et al., 2017; Jullien et al., 2012; Kawakatsu et al., 2017; Moreno-Romero et al., 2019; Narsai et al., 2017; Walker et al., 2018). At specific loci, allelic-specific methylation patterns are also maintained throughout the development and contribute to allelic-specific gene expression in the hybrids, which is related to heterosis in rice (Ma et al., 2021; Shao et al., 2019).

Mutations of DNA demethylase affect the development of embryo and endosperm, which stores nutrient and provides support to the developing embryo (Jia et al., 2020b; Kim et al., 2019; Liu et al., 2018d; Zhou et al., 2021b). In rice, it has been demonstrated that grains of the *Osros1* mutant develop a thicker aleurone layer, which is rich in essential nutrients like proteins, lipids, vitamins, and minerals (Liu et al., 2018d). This enhances the nutritional contents and quality of rice grains. The maize genome encodes four DNA demethylases, *ZmROS1a/b/c/d* (Gent et al., 2022; Xu et al., 2022). Kernels of the double mutants are either small (*ZmROS1ab*) or nonviable (*ZmROS1bd*) (Gent et al., 2022). In addition, maize mutants with perturbed DNA methylation, including *ddm1* and *cmt3*, cannot produce viable kernels due to arrested zygote development (Fu et al., 2018a; Li et al., 2014b; Long et al., 2019).

Histone modifications also play a role in regulating plant embryogenesis and seed development (Kim et al., 2019; Liu et al., 2018d; Zhou et al., 2021b). In Arabidopsis, the maternal chromatin of endosperm exhibits a higher enrichment of H3K27me3, due to the maternal expression of PRC2 core components, FIS2, and MEDEA (MEA) (Luo et al., 2000; Moreno-Romero et al., 2016). Mutations in FIS2 and MEA lead to autonomous endosperm development and the arrestment of ovule development (Chaudhury et al., 1997; Kiyosue et al., 1999; Luo et al., 2000). In rice, the maternally expressed OsEMF2a is essential for endosperm cellularization and imprinting (Cheng et al., 2021b; Tonosaki et al., 2021). Mutation in another rice PRC2 component, OsFIE2, promotes asexual embryo formation.

Other epigenetic modifications involved in endosperm development include miRNAs and histone acetylation. (Hu et al., 2021; Rossi et al., 2007; Song and Chen, 2015; Xu et al., 2023; Yang et al., 2016; Zhang et al., 2022c; Zhou et al., 2021c). Defects and/or altered expression of histone acetyltransfersaes and HDACs lead to abnormal seed development and reduced grain yield in rice and maize (Li et al., 2023b; Rossi et al., 2007; Song and Chen, 2015; Yang et al., 2016). Such effects and functional mechanisms may also be conserved in other Poaceae crops, such as wheat (Zhao et al., 2024; Zhao et al., 2023b).

Vernalization and floral transition

The regulation of flowering time is crucial for plants to adapt to seasonal changes. FLOWERING LOCUS T (FT), a prominent florigen and its upstream regulator, FLOWERING LOCUS C (FLC), are pivotal in this process (Corbesier et al., 2007; Jaeger and Wigge, 2007; Luo and He, 2020; Luo et al., 2021). The

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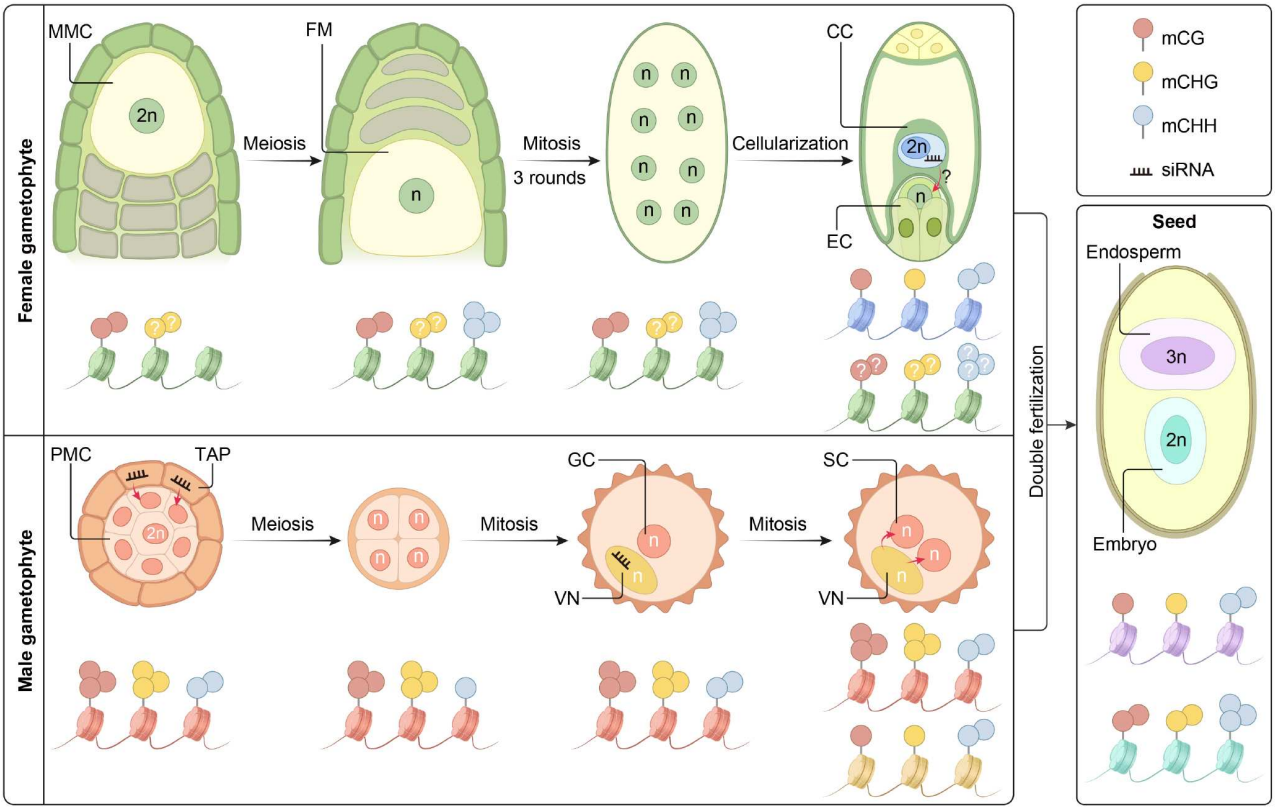

Figure 1. DNA methylation dynamics during plant reproductive development. The subepidermal cell in the ovule differentiates into MMC, while the anther meristem primordia differentiate into PMC. The MMC produces the haploid egg cell and the diploid central cell, whereas the PMC generates two sperm cells and a vegetative cell. After double fertilization, a diploid embryo and a triploid endosperm are produced. The levels of DNA methylation (mCG, mCHG, and mCHH) in various plant cells are represented by the size of different shapes. Red arrows indicate that the siRNAs produced in nurse cells or companion cells guide DNA methylation in the reproductive cells. MMC, megaspore mother cell; FM, functional megaspore; CC, central cell; EC, egg cell; PMC, pollen mother cell; TAP, tapetum; GC, generative cell; SC, sperm cell; VN, vegetative nuclear.

expression of the *FT* gene is repressed by H3K27me3 during the daytime and increases at dusk (Figure 2A). Two repressive complexes LHP1-EMF1c (consists of LIKE HETEROCHROMATIN PROTEIN 1, JMJ14, and EMBRYONIC FLOWER1) and BAH-EMF1c (consists of EARLY BOLTING IN SHORT DAYS, SHORT LIFE, and EMF1) recognize H3K27me3 and interact with the CLF-PRC2 complex, which deposits H3K27me3 (Li et al., 2018b; Wang et al., 2014a; Yang et al., 2018b). H3K4me3 methyltransferases, ATX1, along with the H3K4me3/H3K36me3 readers, MORF RELATED GENE 1 (MRG1) and MRG2, play a role in enhancing the expression of the *FT* gene under long-day conditions to promote flowering (Figure 2A) (Bu et al., 2014; Jing et al., 2019; Xu et al., 2014).

FLC is a MADS-box transcription factor that represses the expression of *FT*, thereby delaying the transition to flowering (Gao and He, 2024; He et al., 2020). In winter annual plants, *FLC* expression is promoted by the FRIGIDA super complex (FRIsc), which consists of RNA polymerase II associated factor 1 (PAF1c), SWR1c, the nuclear pre-mRNA cap-binding complex (CBC), histone 2B mono-ubiquitination (H2Bub1) enzymes UBC1 (UBIQUITIN-CONJUGATING ENZYME 1) and UBC2, HAM1/2, and EFS (Figure 2B) (Li et al., 2018c; Luo and He, 2020; Xu et al., 2022). High expression of *FLC* also promotes seed germination of winter-annual plants in autumn (Chiang et al., 2009). The active chromatin state of *FLC* is maintained during vegetative growth until the plants are exposed to low temperatures.

During vernalization, FRIGIDA (FRI) forms condensates and leads to decreased active histone modifications at *FLC* (Zhang et al., 2023h; Zhu et al., 2021). Additionally, prolonged cold exposure leads to the formation of VIN3-PRC2 complex and its recruitment to the chromatin by VIVIPAROUS1/ABI3-LIKE (VAL) 1 and VAL2, resulting in H3K27me3 deposition (Franco-Echevarría et al., 2023; Li and Cui, 2016; Yuan et al., 2016; Zhao et al., 2020). When the temperature returns to warmth, VIN3 undergoes rapid degradation, and the VRN5-PRC2 complex works collectively with H3K27me3 readers EARLY BOLTING IN SHORT DAY (EBS), SHORT LIFE (SHL), and LHP1 to propagate and preserve H3K27me3 in maintaining a stable Polycomb-repressed state over *FLC* (Gao et al., 2023; Yang et al., 2017a) (Figure 2C).

The epigenetic modifications at *FLC* need to be reset in each generation to ensure proper control of flowering time through vernalization (Liu et al., 2024). While H3K27me3 reprogramming occurs in sperm cells (Borg et al., 2020; Zhu et al., 2023), the repressed state of *FLC* is retained in the egg cells, and passed on to the early embryos (Luo and He, 2020; Luo et al., 2020b). In early embryo development, the pioneer transcription factor LEAFY COTYLEDON 1 (LEC1) binds to the distal *FLC* promoter, creates an open chromatin for interaction with B3-domain transcription factors LEC2, FUS3 (FUSCA 3), and ABI3 (ABSCISIC ACID-INSENSITIVE 3), possibly followed by the disruption of VAL1, VAL2, and Polycomb protein bindings (Tao et al., 2019; Xu et al., 2022). As the embryo undergoes rapid cell divisions during embryogenesis, H3K27me3, inherited maternally from

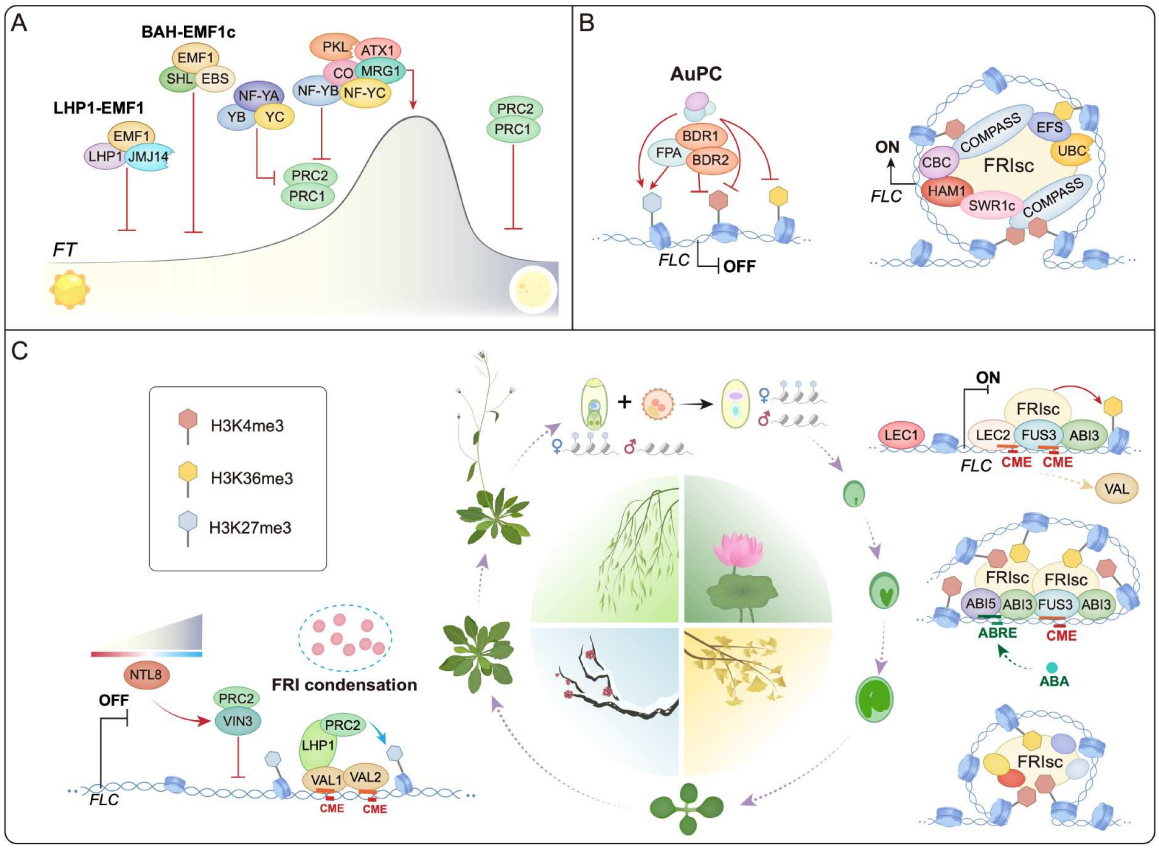

Figure 2. The regulation of *FT* and *FLC* expression mediated by histone modifications in plants. A, Transcriptional regulation of *FT* expression under long-day conditions. B, Transcriptional regulation of *FLC* expression mediated by AuPC and FRIsc. C, Epigenetic regulation of *FLC* expression in response to seasonal changes in Arabidopsis winter annuals.

the vernalized parent, gradually decreases, and the active chromatin state is re-established through the recruitment of the FRIsc complex by LEC2, FUS3, leading to the activation of *FLC* (Tao et al., 2019; Xu et al., 2022).

Plant architecture

It has been proposed that the potential of crop yields can be boosted through the development of plants with ideal plant architecture (IPA), featuring optimal plant height, leaf inclination and size, tiller number, etc. for maximal photosynthetic efficiency and energy conversion rate. In searching for IPA quantitative trait locus (QTL), the *OsSPL14* (SQUAMOSA PROMOTER BINDING PROTEIN-LIKE 14) gene has been identified (Jiao et al., 2011; Miura et al., 2010). A point mutation in *OsSPL14* disrupts the *OsmiR156* binding site, resulting in an 'ideal' plant architecture with reduced tiller number, increased lodging resistance, and enhanced grain yield. In addition, two IPA epialleles, *ipa1-2D* and *WFP*, showing differential DNA methylation among different rice cultivars were identified (Miura et al., 2010; Zhang et al., 2017). In maize, disruption of *ZMET2* (Zea methyltransferase2), responsible for genome-wide mCHG, increased the number of husk leaves (Wang et al., 2024d). Knock down of SET domain protein 128 (SDG128), a H3K4me3 methyltransferase, leads to increased leaf angles (Wang et al., 2021d).

Besides being a key factor of crop photosynthesis rate, plant architecture was also found to affect crop nutrient utilization efficiency, thus offering an important strategy for optimizing crop yield with minimal environmental impact. A genetic screen aimed at increasing nitrogen utilization efficiency identified *ngr5* mutation in rice (Wu et al., 2020). NITROGEN-MEDIATED TILLER GROWTH RESPONSE 5 (NGR5), an APETALA2-domain transcription factor induced by nitrogen, recruits PRC2 to modulate H3K27me3 levels over several branching-inhibitory genes. Increased expression of NGR5 promotes tillering without nitrogen rich fertilizer.

Factors that affect root development directly influence nutrient uptake. Reduced expression of ZmCHB101, the core subunit of the SWI/SNF-type ATP-dependent chromatin remodeling complex in maize, accelerates root growth and increases biomass under low nitrate conditions (Meng et al., 2020). Mutation in *DDM1* leads to shortened and thickened roots, as well as increased tolerance to low-Pi stress (Luo et al., 2023). In maize, Pi deficiency also strongly induces the expression of miR399 (Du et al., 2018; Wang et al., 2023e), a positive regulator of Pi uptake. Overexpressing miR399 or knockout of its target Phosphate 2 (*ZmPHO2*) leads to excessive accumulation of Pi and apparent leaf senescence. Interestingly, ZmmiR399-guided cleavage of *ZmPHO2* is inhibited by *RNAPILNCR1*, a noncoding RNA also induced under Pi deficiency, suggesting a finetuned feedback regulation of low Pi responses in maize (Du et al., 2018).

Regeneration

Plant regeneration through tissue culture provides not only a

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method for vegetative propagation, but also the groundwork for plant improvements through transformation and genetic engineering (Ikeuchi et al., 2019). Using Arabidopsis regeneration as an example, the typical procedure involves callus induction, followed by either shoot or root organogenesis in medium containing proper types and concentrations of phytohormones. Studies in Arabidopsis offered mechanistic insights into the transdifferentiation process of callus induction, revealing its similarity with lateral root formation (Atta et al., 2009; Che et al., 2007; Fan et al., 2012; He et al., 2012; Sugimoto et al., 2011; Sugimoto et al., 2010).

Cell fate transition guided by the epigenetic reprogramming constitutes a key theme during callus formation (Li et al., 2024a; Wu et al., 2022). For example, H3K27me3 levels are upregulated at many leaf-related genes and downregulated at many root-related genes, leading to the transition from leaf to root cell identity (He et al., 2012). HISTONE THREE RELATED 15 (H3.15), an atypical histone variant, promotes pluripotency by removing the H3K27me3 (Yan et al., 2020). HISTONE ACETYLTRANSFERASE1 (HAG1) primes transcriptional activation of several root identity genes including *WUSCHEL-RELATED HOMEOBOX5* (*WOX5*), *SCARECROW* (*SCR*), and *PLETHORA1* (*PLT1*) (Kim et al., 2018). Mutation in *ARABIDOPSIS TRITHORAX4* (*ATX4*) results in reduced shooting capacity due to compromised H3K4me3 deposition at shoot identity genes (Lee et al., 2019).

Understanding the epigenetic programing involved in plant regeneration offers us possible strategies to overcome the genetic and epigenetic constraints that limit plant regeneration and transformation efficiency (Chen et al., 2024). It has been shown that overexpression of certain morphogenic regulators, such as *WUSCHEL* (*WUS*), *BABY BOOM* (*BBM*), and *WOX5*, promotes shoot regeneration in both Arabidopsis and wheat (Wang et al., 2022c; Zhai and Xu, 2021; Zhou et al., 2024). Similarly, DNA BINDING WITH ONE FINGER (DOF) enhances shoot regeneration in wheat tissue culture (Liu et al., 2023d). Based on these knowledge, CRISPR-activation (CRISPR-a) tools have also been developed for targeted activation of endogenous morphogenic regulators (Pan et al., 2022; Zhang et al., 2024). These tools have successfully accelerated plant regeneration in various economically significant plant species such as poplar, alfalfa, sheepgrass, and woodland strawberry (Pan et al., 2022; Zhang et al., 2024). We envision that continued advancements in epigenetic modifications through CRISPR-Cas9 may offer a new venue to a more efficient plant and crop tissue culture system in the future.

Fruit ripening

Ripening directly determines fruit quality and economic values. In tomatoes, a genome-wide investigation at four fruit developmental stages reveals that DNA methylation continuously decreases throughout maturation (Table 1) (Zhong et al., 2013). *SlDML2*, encoding one of the four DEMETER-like DNA demethylases in tomatoes, is highly expressed in fruit and exhibits ripening related expression (Liu et al., 2015). Silencing or knocking out of *SlDML2* delays ripening (Lang et al., 2017; Liu et al., 2015). *SlDML2* transcripts are also regulated by RNA modification. SlALKBH2 removes m^{6}A from and destabilizes *SlDML2* transcripts. Knocking out of *SlALKBH2* delays ripening, further implying the intricate interplay between DNA methylation and m^{6}A modification on RNA (Zhou et al., 2019).

Histone modifications are also implicated in fruit ripening. SlHDA3 and SlHDA1, histone deacetylases belonging to the RPD3/HDA1 subfamily, repress genes in cell wall metabolism and thus delay fruit softening (Guo et al., 2018a; Guo et al., 2017b). Conversely, SlHDT3, a histone deacetylase, promotes softening through modulating ethylene biosynthesis and carotnoid accumulation (Guo et al., 2017a). H3K27me3 and H3K4me3 have also been implicated in the regulation of fruit ripening. For example, overexpression of SlMSI1 (a PRC2 component) or SlLHP1b inhibits ripening (Liang et al., 2020; Liu et al., 2016), while overexpression of SlJMJ6 promotes ripening through H3K27me3 demethylation (Li et al., 2020b). Removal of H3K4me3 by SlJMJ7 inhibits ethylene biosynthetic genes and ripening promoting transcription factors and thus delays ripening (Ding et al., 2022). Finally, it is worth mentioning that ncRNAs are involved in ripening (Gao et al., 2015; Tan et al., 2017; Zhu et al., 2015). A recent review covered over 40 non-coding RNAs and their roles in ethylene biosynthesis, color, taste, and texture during tomato ripening (Ma et al., 2020).

Fruit coloration

Fruit ripening is often associated with changes in color as a result of anthocyanin biosynthesis. Several studies suggest that DNA methylation is involved in fruit coloration. In peach, low methylation within promoters of anthocyanin biosynthesis genes leads to increased transcription at low temperatures. Consistently, chemical inhibition of DNA methylation induces significant accumulation of anthocyanin, indicating that DNA demethylation is crucial in temperature dependent accumulation of anthocyanin post-harvest (Zhu et al., 2020). In European pear, expression of a transcriptional factor *PcMYB10* is repressed by DNA methylation in the promoter. PcMYB10 activates the transcription of *PcUFGT*, which encodes a key enzyme in anthocyanin biosynthesis. Therefore, methylation of *PcMYB10* promoter indirectly leads to green skinned sports (Wang et al., 2013). In radish, white-fleshed epi-mutants are generated due to a hypermethylated CACTA transposon inserted into the promoter of *RsMYB1*, leading to its silencing and the inhibition of anthocyanin accumulation (Wang et al., 2020b). Sweet oranges undergo global gain of DNA methylation during ripening, which is associated with decreased expression of four DNA demethylase genes. Chemical inhibition of DNA methylation represses the coloration of the skin (Huang et al., 2019). In *Vitis vinifera*, the levels of DNA methylation in veraison stage are relatively higher than those in green and mature fruits, and decreased DNA methylation in 3′ LTR of the retrotransposon is associated with an accumulation of anthocyanin in the fruit (Azuma and Kobayashi, 2022; Shangguan et al., 2020). Similarly in apple, genes involved in anthocyanin pathway, such as ANTHOCYANIDIN SYNTHASE (*ANS*) and FLAVONE 3β-DYHDROXYLASE (*F3H*), are differentially methylated and differentially expressed between deep-red-skinned and lighter-skinned apple fruits (Azuma and Kobayashi, 2022; Jiang et al., 2019).

Plant immunity

To defend against the infection of diverse microbial pathogens, plants have developed sophisticated immune mechanisms. A

Table 1. Epigenetic regulations involved in fruit development

Crops	Traits/changes induced	Phenotype	Epigenetic modification	References
Tomato	DNA methylation levels decrease continuously as the fruit matures	Ripening	DNA methylation	(Zhong et al., 2013)
	Decreases in DNA methylation are associated with not only hundreds of ripening-induced genes but also many ripening-repressed genes	Ripening	DNA methylation	(Lang et al., 2017)
	Silencing or knocking out *SlDML2* (DEMETER-like DNA demethylases) delays ripening	Ripening	DNA methylation	(Lang et al., 2017; Liu et al., 2015)
	SlALKBH2 regulates m^6A demethylation levels and subsequently impacts mRNA stability of *SlDML2*; knocking out *SlALKBH2* delays ripening	Ripening	mRNA methylation &DNA methylation	(Zhou et al., 2019)
	SlHDA3 and SlHDA1 negatively regulate fruit softening, SlHDT3 acts as a positive regulator by activating similar genes	Ripening	Histone modification	(Guo et al., 2017a; Guo et al., 2018a; Guo et al., 2017b)
	Overexpression of *SlMSL1* inhibits the expression of the ripening related genes and displays enlarged sepals and non-ripening fruits	Ripening	Histone modification	(Liu et al., 2016)
	SlLHP1b attaches to the H3K27me mark within ripening-associated chromatin regions, affecting ripening-related ethylene biosynthesis, carotenoid biosynthesis, and RIN targeted genes, and suppressing fruit ripening	Ripening	Histone modification	(Liang et al., 2020)
	Overexpression of histone lysine H3K27 demethylase SlJMJ6 accelerates the fruit ripening process	Ripening	Histone modification	(Li et al., 2020b)
	H3K4 demethylase SlJMJ7 may affect fruit ripening by regulating the expression of ethylene biosynthesis genes and ripening related transcription factor genes through H3K4me3 demethylation	Ripening	Histone modification	(Ding et al., 2022)
	Over 40 non-coding RNAs are associated with the ethylene pathway, color, taste, and texture during tomato ripening	Ripening	Non-coding	(Ma et al., 2020)
Peach	DNA demethylation is crucial in temperature dependent accumulation of anthocyanin post-harvest	Coloration	DNA methylation	(Zhu et al., 2020)
Pear	Methylation of *PcMYB10* promoter indirectly leads to green skinned sports	Coloration	DNA methylation	(Wang et al., 2013)
Radish	White-fleshed epi-mutants are generated because a hypermethylated CACTA transposon is inserted into the promoter of *RsMYB1*, leading to its silencing and the inhibition of anthocyanin accumulation	Coloration	DNA methylation	(Wang et al., 2020b)
Oranges	Chemical inhibition of DNA methylation represses the coloration of the skin	Coloration	DNA methylation	(Huang et al., 2019)
Vitis vinifera	The levels of DNA methylation in veraison stage are relatively higher than those in green and mature fruits, and decreased DNA methylation in 3′LTR of the retrotransposon is associated with an accumulation of anthocyanin in the fruit	Coloration	DNA methylation	(Azuma and Kobayashi, 2022; Shangguan et al., 2020)
Apple	*ANS* and *F3H* are differentially methylated and differentially expressed between deep-red-skinned and lighter-skinned apple fruits	Coloration	DNA methylation	(Azuma and Kobayashi, 2022; Jiang et al., 2019)

variety of epigenetic mechanisms, including DNA methylation, histone modifications, and chromatin remodeling have been shown to participate in plant defense against pathogens, and function as positive or negative regulators of plant immunity (Table 2) (Lee et al., 2016; Li et al., 2020a; Roy et al., 2018; Xie et al., 2023b). For example, upon infection by *Pseudomonas syringae* pv. *tomato* strain DC3000 (*Pto* DC3000), ROS1 functions to derepress RdDM targets, and restricts bacterial propagation within xylem vessels. In this example, ROS1 functions as a positive regulator of plant defense through DNA demethylation of the disease resistant genes, *RESISTANCE TO METHYLATED GENE* 1 (RMG1) (Figure 3A) (Yu et al., 2013). In another case, JMJ28 recruits the ATX1/2-COMPASS complex to chromatin for H3K4 methylation deposition and functions as a negative regulator of plant immunity (Xie et al., 2023b). Several chromatin remodelers (such as SWP73A/BAF60, CHR5, DDM1, and SYD) have been revealed in maintaining the homeostasis of NOD-like immune receptors (NLRs), such as SUPPRESSOR OF NPR1-1, CONSTITUTIVE 1 (SNC1), to prevent autoimmune responses (Figure 3B) (Huang et al., 2021a; Johnson et al., 2015; Li et al., 2010; Yang et al., 2023c; Zou et al., 2017).

The regulation of plant defense genes by epigenetic regulators can be either direct or indirect (Lee et al., 2016). For example, through chromatin immunoprecipitation (ChIP) assay, *WRKY70* was found to be a direct target of H3K4me3 methyltransferase ATX1, while *PR1* and *THI2.1* appeared to be secondary targets (Alvarez-Venegas et al., 2007). Adding to the complexity, it has been shown that epigenetic regulators can impose multiple layers of epigenetic modifications in regulating plant defense. For example, in Arabidopsis *sdg8* and *sdg25* mutants, not only H3K4 and H3K36 histone lysine methylations were reduced over two defense genes, *CAROTENOID ISOMERASE2* (*CCR2*) and *ECERIFERUM3* (*CER3*), H2B ubiquitination was also impaired at these two loci, suggesting a cross talk between different types of histone modifications in regulating plant immunity (Lee et al., 2016).

Plants mainly utilize two complementary signaling pathways,

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Table 2. Epigenetic regulators involved in plant immunity

Plants	Pathogens	Epigenetic regulators	Epigenetic modifications	Defense genes	References
Arabidopsis	*Pst* DC3000	RdDM, ROS1	DNA methylation	SA mediated defense responses, *Resistance Methylated Gene 1 (RMG1)*	(Yu et al., 2013)
		RdDM	–	–	(Luna and Ton, 2012)
		DDM1	–	*GPK1* (*GLYOXYSOMAL PROTEIN KINASE 1*)	(Lee et al., 2023)
		CAF-1	Chaperone H3K4me3	SA mediated defense responses	(Mozgová et al., 2015)
		JMJ14	H3K4 methylation	*SNI1* (*SUPPRESSOR OF NPR1-1 INDUCIBLE 1*)	(Lee et al., 2016; Li et al., 2020a)
		FLD, LDL1, LDL2	H3K4me3	WRKY transcription factors	(Banday and Nandi, 2018; Noh et al., 2021; Singh et al., 2014b)
		LHP1	H3K27me3	*MYC2*	(Ramirez-Prado et al., 2019)
		JMJ27	H3K9me2	*PR* (*PATHOGENESIS RELATED*) genes	(Dutta et al., 2017)
		ATX1	H3K4me3	*WRKY70*	(Alvarez-Venegas et al., 2007)
		GCN5	H3K14Ac	SA-responsive defense genes	(Kim et al., 2020)
		SUVH4/5/6	H3K9me2	*PRR* (*PATTERN RECOGNITION RECEPTORS*), *NLR*	(Cambiagno et al., 2021)
		HAC1, HAC5	Histone Acetylation	*NPR1*, *TGA*, *PR* genes	(Jin et al., 2018)
		SWP73A/BAF60	Nucleosome organization	*SNC1*	(Huang et al., 2021a)
		CHR5, DDM1, SYD	–	–	(Yang et al., 2023c; Zou et al., 2017, Li et al., 2010, Johnson et al., 2015)
		HDA6	Histone acetylation	*CBP60g* (*CALMODULIN BINDING PROTEIN 60g*), *SARD1* (*SYSTEMIC ACQUIRED RESISTANCE DEFICIENT 1*)	(Wu et al., 2021)
	Verticillium dahlia, *Botrytis cinerea*	JMJ28, ATX1/2-COMPASS	H3K4 methylation	–	(Xie et al., 2023b)
	Botrytis cinerea, *Pst* DC3000	MEA	H3K27me3	*RPS2* (*RESISTANCE TO P.SYRINGAE2*)	(Roy et al., 2018)
	Bacterial pathogens, insects	–	Histone Acetylation	JA-responsive genes	(Zhang et al., 2017)
	Botrytis cinerea	GCN5, HDA6	Histone Acetylation	*TPL*, *NINJA*, *MYC2* target genes	(An et al., 2022)
	Necrotrophic fungal pathogens	HUB1, HUB2	H2Bub1	*SNC1*	(Dhawan et al., 2009; Yang et al., 2023c; Zou et al., 2014)
	Sclerotinia sclerotiorum	SWR1	H2A.Z, H3K4me3	*YDD* (*YODA DOWNSTREAM*)	(Cai et al., 2021)
Rice	Blast fungus	RdDM	DNA methylation	*Pigm* locus	(Deng et al., 2017)
	Magnaporthe oryzae	lsiR76113	–	*CNGC5*	(Zheng et al., 2024)
Maize	*Fusarium graminearum*	–	H3K27me3, H3K9me3, H3K4me3, DNA methylation	*qRfg1*	(Wang et al., 2017)
	Southern leaf blight	ZmAGO18b	–	–	(Dai et al., 2023)
Pepper	*Ralstonia solanacearum*	CaSWC4	Histone modification	–	(Cai et al., 2021)

the jasmonate (JA) and salicylic acid (SA) pathways, to defend themselves against necrotrophic and biotrophic pathogens, respectively. Epigenetic regulators function to regulate the balance between these two pathways (Figure 3C). Under normal growth condition, JAZ, TOPLESS (TPL), and NINJA (NOVEL INTERACTOR OF JAZ) constitute a repressor complex that suppresses the expression of JA-responsive genes (Zhang et al., 2017). The interaction between TPL and NINJA is enhanced by GENERAL CONTROL NON-DEREPRESSIBLE 5 (GCN5), which directly acetylates TPL (An et al., 2022). Additionally, HDA6 counteracts the function of GCN5 through TPL deacetylation, which weakens TPL-NINJA interaction and allows for transcriptional activation of JA-responsive genes (An et al., 2022). As for SA signaling pathway, HAC1 and HAC5 form complexes with NONEXPRESSOR OF PATHOGENESIS RELATED GENES 1 (NPR1) and TGACG-BINDING FACTOR (TGA) in mediating SA-triggered immunity through activation of pathogenesis-related genes (PR genes) (Jin et al., 2018) (Figure 3C).

In plants, defense priming refers to a physiological process by which a plant prepares itself for a much faster and stronger immune response when the same type of pathogenic attack reoccurs. It has been shown that the activation of plant defense genes was repressed in the *hac1* mutant, indicating the contribution of histone acetylation to defense priming (Singh et al., 2014a) (Figure 3D). In contrast, histone chaperone CHROMATIN ASSEMBLY FACTOR 1 (CAF-1) is required for maintaining defense genes in a repressed state (Mozgová et al., 2015). In the *caf1* mutant, the SA-dependent defense response is spuriously activated under non-inductive conditions, resembling the primed condition. In addition, DNA methylation pathways were also found to regulate the priming of plant defense genes (Lee et al., 2023; Luna and Ton, 2012).

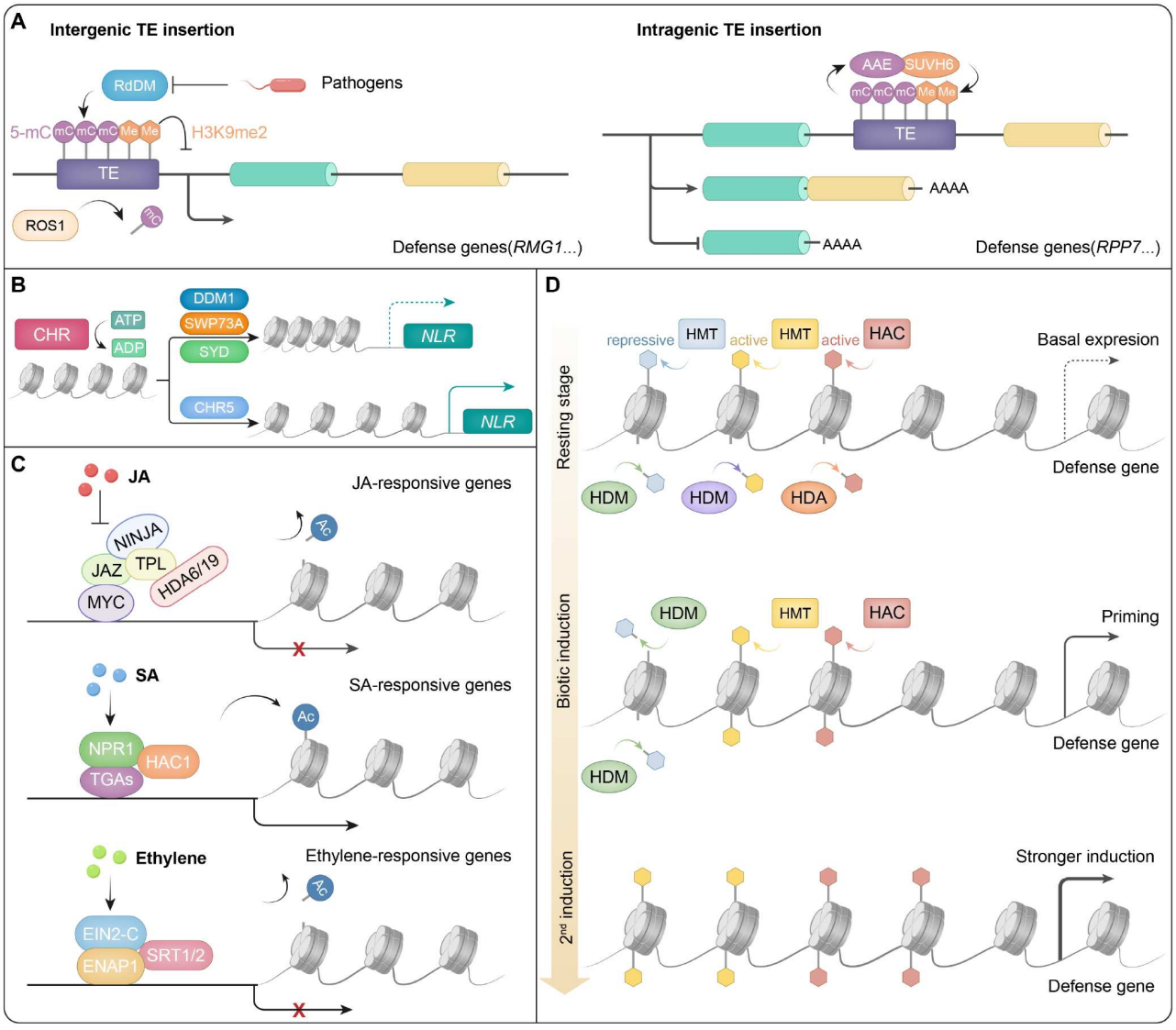

Figure 3. Chromatin-based regulation of plant immunity. A, Effects of DNA methylation and TE insertion on defense gene expression. B, Chromatin remodeler-mediated regulation of the homeostasis of NLR immune receptors. C, Histone acetylation and defense immune signaling. D, A working model of epigenetic regulation of defense priming and memory.

In addition, plants and pathogens both utilize small RNA silencing machinery as a weapon to defend each other (Boccara et al., 2014; Deng et al., 2018; González et al., 2015; Li et al., 2012; Lopez-Gomollon and Baulcombe, 2022; Shivaprasad et al., 2012a; Zhai et al., 2011). These small RNAs were found to translocate in-between the pathogens and host plants, a phenomenon known as trans-kingdom RNAi (Liu et al., 2023c) (Figure 4). The trans-kingdom regulation by small RNAs is bidirectional, referred to as host-induced gene silencing (HIGS) and pathogen-induced gene silencing (PIGS), respectively (Cai et al., 2018; Weiberg et al., 2013). For instance, plants can deliver *miR159* and *miR166* to the pathogenic fungus *Verticillium dahliae* to silence fungal virulence genes, thereby antagonizing fungal infection (Zhang et al., 2016c). Meanwhile, pathogens can produce a type of protein known as the suppressor of trans-kingdom RNAi (STR), which translocates into the plant nucleus, and prevents the nuclear export of the miRNA-AGO1 complex and the accumulation of mobile miRNAs (Hou et al., 2019; Qiao et al., 2013; Zhu et al., 2022). Additionally, viruses have evolved viral suppressors of RNA silencing (VSRs) to counteract the plant RNA silencing pathways at various stages (Duan et al., 2012; Lopez-Gomollon and Baulcombe, 2022).

Gibberella stalk rot in maize is a devastating disease caused by *Fusarium graminearum*. The gene *ZmCCT* was identified as a quantitative locus that confers resistance in maize (Wang et al., 2017). The insertion of polymorphic CACTA-like transposon upstream of *ZmCCT* attracts DNA methylation, and causes *ZmCCT* transcriptional silencing and disease susceptibility (Wang et al., 2017). Besides epigenetic modification in *cis*, crops can also respond to pathogen infection through small RNA pathways. For example, maize ZmAGO18b was found to negatively regulate southern leaf blight (Dai et al., 2023). In rice, long small RNA (lsiR76113) is downregulated by rice blast fungus (*Magnaporthe oryzae*) infection, leading to an increased expression of its targeting gene *CNGC5* and enhanced disease resistance (Zheng et al., 2024). In crops, there is often a trade-off between the

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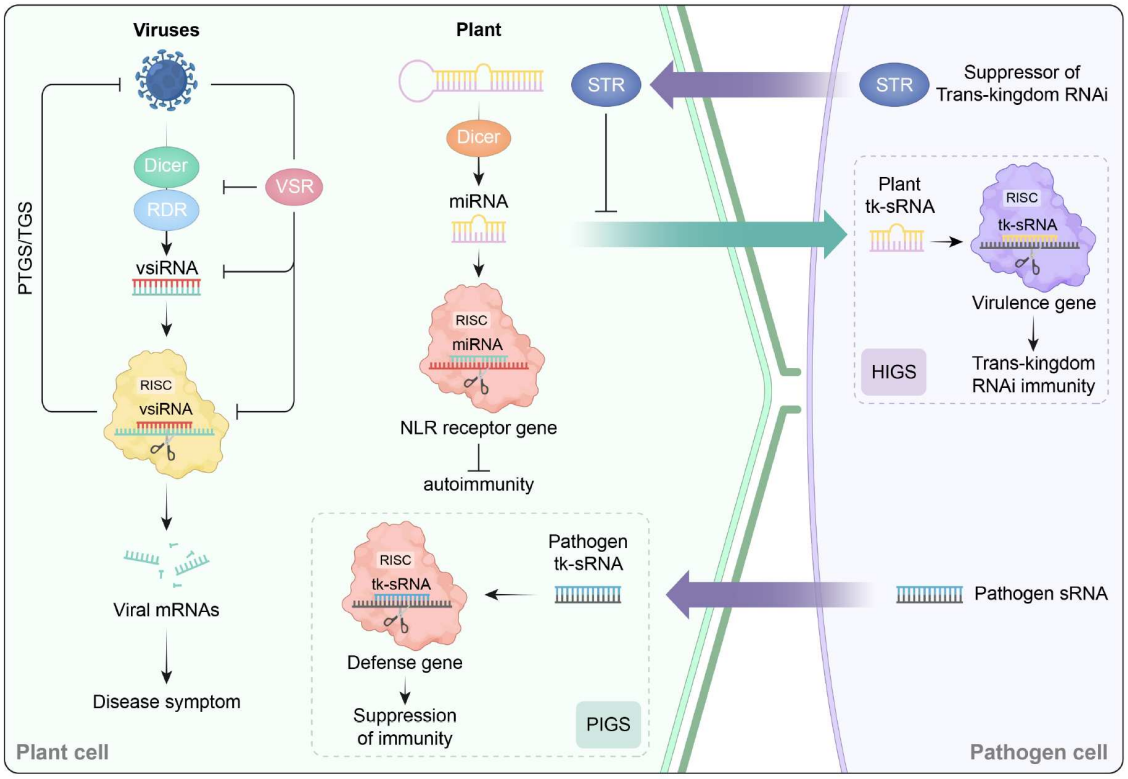

Figure 4. Small RNA-mediated viral and non-viral plant immunity. STR, suppressor of trans-kingdom RNAi. Tk-sRNA, trans-kingdom sRNA. RDR, RNA-dependent RNA polymerase.

disease resistance and yield. A recent study has discovered that the resistance (R) genes of the rice *Pigm* locus are epigenetically regulated in an organ specific manner, allowing tissue specific defense response against *Magnaporthe oryzae* infection without causing yield penalty (Deng et al., 2017). This result suggests a novel strategy for developing disease resistant crops by modulating the expression of disease resistant genes in a tissue specific manner.

Nodulation

Microbes can form symbiotic relationships with crops. One notable example is the fixation of atmospheric nitrogen through the symbiotic relationship between legumes and nitrogen-fixing rhizobia, which not only has ecological significance but also is pivotal for sustainable agricultural production.

In *Medicago truncatula*, reducing the activity of DME leads to hypermethylation and the subsequent down-regulation of nodulation differentiation genes, resulting in pronounced nodule developmental defects (Satgé et al., 2016). In addition, extensive research has highlighted the role of non-coding RNAs, particularly small RNAs, in regulating nodule development (Hoang et al., 2020). For instance, Gm-miR4416, a miRNA specific to soybean, targets rhizobium-induced peroxidase (RIP1)-like peroxidase genes to regulate nodule number (Yan et al., 2016).

As small RNAs are mobile between microbe and its host plant and within the plant itself, the regulation of nodulation can occur through both local trans-kingdom interactions or through systemic mechanism known as autoregulation of nodulation (AON) (Caetano-Anollés and Gresshoff, 1991). For example, it has been shown that small RNAs derived from rhizobial tRNA fragments hijack soybean AGO1b to target soybean genes involved in root hair development, and thereby promote nodulation by root hair deformation (Ren et al., 2019). In the case of AON, Clavata3-like (CLE) peptides are produced in roots in response to rhizobia infection and travel to the shoot to negatively regulate miR2111 biosynthesis. miR2111 is then translocated back to the root, where it suppresses the root-expressed receptor kinase "Too Much Love (TML)", a negative regulator of nodule formation (Tsikou et al., 2018; Zhang et al., 2021b).

Moreover, evolutionarily conserved miRNAs exhibit species-specific functions in soybean nodulation. For instance, while Arabidopsis miR172 targets the AP2 (APETALA2) transcription factors to regulate floral transition and flower development (Chen, 2004), the soybean miRNA172c not only targets the shoot-derived transcriptional repressor GmTOE4a to promote FT expression and flowering (Zhao et al., 2015), but also targets transcription factor Nodule Number Control1 (NNC1), activating the early nodulin gene ENOD40 to promote nodule primordium formation (Wang et al., 2014b). The dual function of miRNA172c also suggests a connection between nodulation and flowering. Supporting this notion, it has been observed that in soybeans, the formation of nodules escalates during vegetative growth and peaks during the flowering stage (Yun et al., 2023).

Heat stress

Temperature is a major environmental factor determining crop yield and distribution. The ability of crops to properly and efficiently respond to extreme temperatures, including both heat and cold, is a key trait for crop breeding. Heat stress induces

global epigenetic changes in chromatin, including alterations in DNA methylation, histone modification, and chromosomal interactions (Table 3) (Li et al., 2021a; Ma et al., 2018; Niu et al., 2022; Sun et al., 2020a; Yang et al., 2023b). These changes can lead to the disruption of heterochromatin and the reactivation of TEs, thereby causing genome instability (Ito et al., 2011; Liang et al., 2021). Under heat stress, the repression of the ONSEN retrotransposon requires mCHH methylation (Liu et al., 2021b), whereas the repression of pericentromeric Gypsy elements requires the linker histone H1. Intriguingly, the loss of DNA methylation enhances heat tolerance, and this effect is further amplified by the loss of H1 (Liu et al., 2021b). These results suggest that TE reactivation under heat stress should not be simply viewed as the damaging consequence, but also as a survival strategy that aids in plant adaptation to heat stress. The observation that Arabidopsis mutants lacking CMT2 also exhibit increased heat stress tolerance further supports this notion (Shen et al., 2014). However, the physiological significance of DNA methylation in heat tolerance appears to be complex, as defects in the RdDM pathway lead to hypersensitivity to heat stress (Popova et al., 2013).

To prepare for the upcoming heat stress, plants have evolved priming strategies, which involve epigenetic modifications at heat response genes (Oberkofler et al., 2021; Zhao et al., 2019d). For example, when plants experience heat, pre-existing H3K4me2 and H3K4me3 persist on heat-shock genes, which likely depends on a slower turnover rate of the histone variant H3.3 (Liu et al., 2018c; Pratx et al., 2023). Heat stress priming also involves JMJ-mediated demethylation of H3K27me3 at heat shock protein (HSP) genes, such as *HSP22* and *HSP17.6C* (Yamaguchi et al., 2021). FORGETTER1 (FGT1) is a PHD domain protein that directly interacts with chromatin remodeling proteins. FGT1 has been found to mediate heat stress memory through the alteration of nucleosome positioning (Brzezinka et al., 2016).

It is evident that the impact of heat on epigenetic changes exhibits locus-specificity. However, how this specificity is achieved remains an open question. One possible mechanism to ensure target specificity is through the function of small RNAs, particularly microRNAs, which are key players in plant heat responses (Zuo et al., 2021). For instance, heat induces miR160, whose overexpression in Arabidopsis enhances seed germination and seedling survival under heat stress (Lin et al., 2018). Other miRNAs involved in heat tolerance include miR398 and miR156 (Fang et al., 2019; Guan et al., 2013; Stief et al., 2014). Additionally, small RNAs can also mediate heat memory (Zuo et al., 2021). An example is the reduced production of tasiRNAs from the *TAS1* and *TAS2* genes in the heat-stressed Arabidopsis plants and their unstressed offsprings (Liu et al., 2019b). This reduction in tasiRNA accumulation leads to an increased accumulation of its downstream target, the *HEAT-INDUCED TAS1 TARGET* (*HTT*) genes, which contributes to enhanced thermotolerance (Li et al., 2014c).

The function of tasiRNA in mediating transgenerational heat memory is further regulated by histone modifications (Liu et al., 2019b). Specifically, HEAT SHOCK TRANSCRIPTION FACTOR A2 (HSFA2) directly activates *Relative of Early Flowering* (*REF6*) expression, which in turn, further activates *HSFA2* expression by removing H3K27me3, forming a feedback loop. This loop maintains the expression of an E3 ubiquitin ligase SGIP1, to ensure SUPRESSOR OF GENE SILENCING (SGS3) degradation in progeny cells (Liu et al., 2019b). SGS3 is required for the biogenesis of tasiRNAs, which target positive regulators of heat tolerance (Li et al., 2014c).

In crops, small RNAs were also found to regulate the balance between heat tolerance and other agronomic traits, such as disease resistance and nutrient assimilation. For example, tasiRNA-ARFs negatively regulate *Auxin Response Factors* (*ARFs*), which coordinate the balance between heat tolerance and disease resistance at vegetative stage (Gu et al., 2023). Moderate attenuation of this tasiRNAs-ARFs regulon, as a result of weak *ago7* mutation, leads to high temperature induced female sterility. Introduction of this *ago7* allele to restorer lines can endow fully mechanized hybrid rice breeding (Li et al., 2022b).

Cold stress

Cold resistance in plants involves various epigenetic regulations at both DNA and histone levels. Variation in DNA methylation at the promoter of *INDUCER OF CBF EXPRESSION 1* (*ICE1*), a central regulator in cold responses, is correlated with phenotypic variations in freezing tolerance observed in Arabidopsis accessions from different latitudes (Xie et al., 2019). Consistently, treatment with DNA methylation inhibitors or loss of DRM2 enhances freezing tolerance (Xie et al., 2019). DNA methylation at the promoter of *ALLANTOINASE* (*ALN*), which encodes a negative regulator of dormancy, is stimulated by cold in a tissue-specific manner through non-canonical RdDM, leading to seed dormancy (Iwasaki et al., 2019). In rubber tree *Hevea brasiliensis*, prolonged cold treatment induces DNA hypomethylation at promoters of cold responsive genes including *HbICE1* and *HbCBF2* (Tang et al., 2018).

In addition, histone modifications have also been implicated in cold stress responses in crops (Kamble, 2024; Qi et al., 2023; Sun et al., 2024b). Cold induces histone acetylation through HOS15 mediated HD2C degradation (Park et al., 2018). In banana, cold induces histone acetylation at the promoters of fatty acid desaturases (FADs), which increase the production of unsaturated fatty acids to maintain membrane integrity (Song et al., 2019). Consistently, HDA6 is required for cold acclimation and freezing tolerance in Arabidopsis (To et al., 2011).

The role of noncoding RNAs in cold stress responses is less explored despite of being crucial. For instance, the lncRNA SVALKA represses C-REPEAT BINDING FACTOR (CBF) 1 expression, and its knockout enhances cell survival under freezing stress after acclimation (Kindgren et al., 2018). Moreover, cold-responsive miRNAs also have been identified and miR169 confers cold tolerance by regulating auxin biosynthesis (Aslam et al., 2020). Recent studies show that AGO1d, induced at low temperatures, mediates the production of reproductive phasiRNAs to maintain male fertility at low temperatures in rice (Shi et al., 2022; Si et al., 2023; Tamotsu et al., 2023).

Drought stress

Under drought condition, dehydration-responsive genes exhibit altered expression, which is associated with changes in different histone modifications (Shi et al., 2023). For example, while H3K4me3 abundance exhibits dynamic changes at dehydration-responsive genes, levels of H3K4me2 and H3K4me1 remain relatively stable (van Dijk et al., 2010). As proposed in the above sessions, stress induced changes in epigenetic modifications

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Table 3. Epigenetic regulators involved in abiotic stresses

Plant species	Stress	Epigenetic modification	Epigenetic regulator	Target	References
Maize	Nitrogen deficiency	H3K27me3	PRC2 complex	–	(Meng et al., 2020)
	Phosphate deficiency	DNA methylation	DDM1	–	(Luo et al., 2023)
		miRNA	miR399	–	(Wang et al., 2023e)
Arabidopsis	Heat stress	DNA methylation	CHH methylation/RdDM	*ONSEN*	(Liu et al., 2021b)
		DNA methylation	CMT2	–	(Shen et al., 2014)
		Nucleosome organization	FGT1	–	(Brzezinka et al., 2016)
		miRNAs	miR160/398/156	–	(Lin et al., 2018; Fang et al., 2019; Guan et al., 2013)
		DNA methylation	NRPD2	–	(Popova et al., 2013)
		H3K27me3	JUMONJI	*HSP22* and *HSP17.6C*	(Yamaguchi et al., 2021)
	Heat stress memory	H3K27me3	REF6	*SGIP1*	(Liu et al., 2019b)
	Cold dependent dormancy	DNA methylation	Non-canonical RdDM	*ALN*	(Iwasaki et al., 2019)
	Cold acclimation	lncRNA	SVALKA	*CBF1*	(Kindgren et al., 2018)
	Drought stress	H3K4me3	ATX1	ABA biosynthesis gene, *NCED3*	(Ding et al., 2011a)
		H3K4me3	ATX4, ATX5	*AHG3*	(Liu et al., 2018e)
		H3K4me3	AtBRCA1	ROS homeostasis	(Wang et al., 2020a)
		H3K27me3	LHP1	*ANAC055*	(Fu et al., 2018b)
		Histone deacetylation	PWR, HDA9, ABI4 complex	ABA pathway	(Khan et al., 2020)
		Nucleosome dynamics	BRAHMA	*ABI5*	(Han et al., 2012)
	Drought stress memory	H3K4me3 and H3K27me3	–	–	(Liu et al., 2014a)
		H3K4me3 and H3K9ac	–	Drought-responsive genes, including *RD29A* and *RD29B*	(Ding et al., 2012; Kim et al., 2012)
	Transgenerational drought memory	DNA methylation	–	–	(Van Dooren et al., 2020)
	Salt stress	miRNAs	miR172	*IDS1* (*INDETERMINATE SPIKELET1*)	(Cheng et al., 2021a)
		Histone acetylation	GCN5	Cell wall biosynthesis genes	(Zheng et al., 2019a)
		Histone deacetylation	HDA4/14/15/18	–	(Ueda et al., 2017; Ueda et al., 2019)
		Histone deacetylation	HDA19	*ANAC019*, *P5CS1*, *LEA4*	(Ueda et al., 2017)
		Histone deacetylation	HD2C	*ABI1*, *ABI2*, *AtERF4*	(Luo et al., 2012)
		sRNA	RDR2 mediated	*HKT1*	(Baek et al., 2010)
Cotton	Heat stress	DNA methylation	–	–	(Ma et al., 2018)
Pepper	Heat stress	Histone modification	CaSWC4	–	(Zhang et al., 2023g)
	Heat stress memory	H3K4me2/3	–	–	(Yamaguchi et al., 2021)
	Transgenerational heat memory	tasiRNAs	TAS1, TAS2	*HTT*	(Li et al., 2014c)
	Heat stress and pathogen response balance	tasiRNAs	ARFs	–	(Gu et al., 2023)
	Cold stress	DNA methylation	–	*ICE1*	(Xie et al., 2019)
		Histone acetylation	HOS15 mediated HD2C degradation	–	(Park et al., 2018)
		miRNAs	miR169	Auxin biosynthetic genes	(Aslam et al., 2020)
		H3K4me3	JMJ17	*OST1* (*OPEN STOMATA*) etc	(Huang et al., 2019)
Potato	Cold stress	H3K4me3/H3K27me3	–	–	(Guo et al., 2023b; Zeng et al., 2019)
Rubber tree	Cold stress	DNA methylation	–	Cold responsive genes including *HbICE1*, *HbCBF2*	(Tang et al., 2018)
Banana	Cold stress	Histone acetylation	–	*FADs*	(Song et al., 2019)
Wheat	Salt stress	DNA methylation	–	*TaHKT2;1*, *TaHKT2;3*	(Kumar et al., 2017)
Rice	Fertility at low temperature	sRNA	AGO1d mediated production of pha-siRNA	–	(Shi et al., 2022; Si et al., 2023; Tamotsu et al., 2023)
		H3K4 methylaiton	SDG721	*OsHKT1;5*	(Liu et al., 2021c)
		Histone deacetylation	HDAC10	*OsHKT2;1*	–
		Histone deacetylation	OsHDA706	*OsPP2C49*	(Liu et al., 2023a)
		H3K4me3	SNAC1-OsERF103-OsSDG705	*OsbZIP23*	(Yang et al., 2024)

enhance plant adaptation. One example is ATX1, the Arabidopsis H3K4me3 methyltransferases. Its binding to ABA biosynthesis gene *NCED3* (*NINE-CIS-EPOXYCAROTENOID DIOXYGENASE 3*) increases under drought condition, which positively regulates drought tolerance (Ding et al., 2011a). In contrast, ATX4 and ATX5 have opposing functions and suppress ABA signaling by activating the key negative regulator *ABA-HYPERSENSITIVE GERMINATION 3* (*AHG3*) (Liu et al., 2018e). The H3K4me3 reader, AtBRCA1 (breast cancer susceptibility gene 1) participates in the regulation of ROS homeostasis during drought stress (Wang et al., 2020a).

Like ATX1, many epigenetic regulators function in plant drought responses through modulating ABA signaling pathway genes, including *RESPONSIVE TO DESSICATION 20* (*RD20*), *ANAC055*, and *ABI5*. For example, both LHP1 and CALCIUM UNDERACCUMULATION 1 (CAU1) repress *ANAC055* expression (Ramirez-Prado et al., 2019). Under drought stress, CAU1 level decreases and the repression on *ANAC055* is released, leading to increased proline biosynthesis and drought tolerance (Fu et al., 2018b). BRAHMA (BRM), a SWI2/SNF2 chromatin remodeling ATPase, directly binds to *ABI5*, modulating nucleosome stability and *ABI5* transcription (Han et al., 2012). However, epigenetic regulation of plant drought responses through ABA pathway-independent genes is also seen (Ding et al., 2011a).

In addition to regulating the primary drought stress response, epigenetic modifications also participate in modulating drought stress memory. H3K4me3 and H3K27me3 modifications are usually associated with transcriptionally active and inactive genes, respectively. However, they were found to coexist on dehydration stress memory genes and function independently (Liu et al., 2014a). Following rehydration, the persistence of H3K4me3 modification over dehydration response genes may be crucial for keeping drought stress memory. Under drought conditions, H3K4me3 and H3K9ac rapidly increase at drought-responsive genes, including *RD29A* and *RD29B*. During recovery, H3K9ac is removed quickly, whereas H3K4me3 persists longer (Kim et al., 2012). The persistence of H3K4me3 not only maintains the basal level transcription of these stress response genes, but also allows a faster and stronger transcriptional activation in subsequent drought stresses (Ding et al., 2012; Kim et al., 2012). The epigenetic mechanism of plant transgenerational drought stress memory remained less understood. Genome-wide analysis of DNA methylation in Arabidopsis suggests that mild drought induces changes in the DNA methylome despite not being heritable (Van Dooren et al., 2020). Consistently, transgenerational drought memory does not correlate with these differentially methylated regions (DMRs) (Ganguly et al., 2017).

Salt stress

To cope with salt stresses, plants employ a number of physiological responses that involve multiple epigenetic regulations, including DNA methylation, histone modification, and small RNA regulation (Feng et al., 2016; Lin et al., 2022; Liu et al., 2023a; Sun et al., 2020b; Ueda et al., 2017; Ueda et al., 2019). For example, miR172 is induced by salt stress and positively regulates rice salt tolerance by repressing the expression of transcription factor INDETERMINATE SPIKELET1; this regulon could fine-tune the expression of a large group of enzymatic ROS-scavenging genes and ROS homeostasis during salt stress (Cheng et al., 2021a). GCN5 promotes cell wall integrity under salt stress by H3K9ac and H3K14ac deposition at cell wall synthesis genes including *CHITINASE-LIKE 1* (*CTL1*), *POLYGALACTURONASE INVOLVED IN EXPANSION-3* (*PGX3*), and *MYB54* (Zheng et al., 2019a).

High-affinity potassium transporters (HKTs) constitute a key salt response gene family, which maintains sodium-potassium homeostasis under salinity stress and is shown to be epigenetically regulated in plants (Byrt et al., 2014; Huang et al., 2008; James et al., 2006). In Arabidopsis, a putative small RNA targeted region approximately 2.6 kb upstream of *HKT1* is heavily methylated (Baek et al., 2010). This methylation is attenuated in RdDM mutant *rdr2*, with a concomitantly higher *AtHKT1* expression. Salt treatment also induces the shortening and fractionation of the H3K27me3 deposition island, further releasing *AtHKT1* from repression and permitting its faster activation upon repeated salt stress (Sani et al., 2013). In wheat, salt-induced DNA methylation at *TaHKT2;1* and *TaHKT2;3* promotes tolerance by down-regulating their expression (Kumar et al., 2017). In rice, histone H3K4 methyltransferase SDG721 promotes salt tolerance through the upregulation of *OsHKT1;5* (Liu et al., 2021c), whereas HDAC10 and OsPPR73 form a repressive complex in repressing *OsHKT2;1* in the presence of salt stress (Wei et al., 2021). Moreover, in plants, epigenetic modifications over *HKT* genes appear to be developmental stage- and tissue-specific (Kumar et al., 2017; Sani et al., 2013). For example, variations in DNA methylation are associated with tissue- and genotype-specific expressions of *TaHKT2;1* and *TaHKT2;3* in the two varieties, Kharchia-65 and HD-2329, with contrasting salinity tolerance (Kumar et al., 2017).

Polyploidization

Polyploidy, characterized by more than two full sets of chromosomes, is a significant driver of crop evolution and domestication (Jiao et al., 2011). Epigenetic modifications play a pivotal role in regulating gene expression in polyploids to overcome the genomic conflicts and generate novel traits through asymmetric expression of duplicated genes (Ding and Chen, 2018; Song and Chen, 2015).

Hexaploid wheat (AABBDD) experienced two rounds of hybridizations. The first round took place between diploid *Triticum urartu* (AA) and an unknown B genome donor, followed by a second round between *Triticum turgidum* (AABB) and *Aegilops tauschii* (DD) (Xiao et al., 2022). Genomic shock occurred immediately after each polyploidization event (Sha et al., 2023), prompting epigenetic regulations to reprogram gene expression and ensure genome stability (Lloyd and Lister, 2022). Studies have indicated the importance of H3K27me3 homeostasis and the function of LHP1 in regulating allele-specific gene expression and subgenome-divergence associated with wheat agronomic traits, such as disease resistance (Li et al., 2023e; Li et al., 2023e; Wang et al., 2021c). There is also a concurrent increase in the level of H3K27me2 and ploidy during wheat evolution. Wheat H3K27me2 tends to co-localize with the CACTA family transposon, indicating its role in transposon silencing and maintaining genome integrity (Liu et al., 2021d).

In addition to histone modifications, DNA methylation changes manifest in newly formed wheat polyploids (Yuan et al., 2020). For instance, hypo-DNA methylation in the promoter regions of root hair development genes and nitrogen transporter

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genes was observed in synthetic allotetraploid wheat (S^lS^lAA). This likely contributes to elongated root hairs and enhanced nitrogen uptake and assimilation compared with the diploid donors TL05 (S^lS^l, *Aegilops longissima*) and TMU06 (AA, *Triticum urartu*) (Miao et al., 2024).

Soybean (*Glycine max*) experienced two rounds of whole genome duplications (WGD) approximately 59 and 13 million years ago (MYA) (Schmutz et al., 2010). The second WGD was specific to *Glycine* genus, but not its close relative, common bean (*Phaseolus vulgaris*). There was a dramatic change in chromatin 3D arrangements during soybean polyploidization (Wang et al., 2021a). Moreover, approximately 75% of soybean genes exist as multiple copies due to WGD (Schmutz et al., 2010; Wang et al., 2012). Compared with singletons and small-scale duplicated genes, WGD genes feature more long-range chromosomal interactions, higher levels of active histone marks, and chromatin accessibilities (Wang et al., 2021a). CG gene body methylation was also abundant in WGD genes (Kim et al., 2015). To properly interrogate the role of epigenetic variations in regulating gene expression, it is crucial to differentiate pure epigenetic variations from those associated with genetic variations. It has been shown that among DMRs identified among different soybean cultivars, around 22.54% can be explained by genetic variations, and those pure DMRs are enriched in carbohydrate metabolism pathways (Shen et al., 2018).

Domestication

Epigenetic variations have been implicated in regulating differential agronomic traits during crop domestication (Guo et al., 2023a). Studies on 104 wheat varieties showed that DNA methylation patterns correlated significantly with their geographic origins and traits such as heading date and salt tolerance (Gardiner et al., 2018). Comparison between nitrogen-efficient and -inefficient wheat cultivars suggest that histone modifications like H3K27me3, H3K27ac, and H3K4me3 have a higher variation and stronger association with the expression of nitrogen metabolism genes than DNA sequences (Zhang et al., 2023b). Consistent with this notion, disruption of the H3K27me3 methyltransferase, *TaSWN*, led to altered nitrogen uptake efficiency in response to low nitrogen (Zhang et al., 2023b; Zhang et al., 2023c).

In addition, previous studies also revealed a differential regulation by microRNAs during wheat domestication (Shen et al., 2018). The *Q* gene influences key traits including seed dispersal and plant architecture (Jantasuriyarat et al., 2004). The transition from non-free-threshing wild varieties to free-threshing domesticated varieties involved a critical missense mutation within *Q* gene at an miR172 binding site, attenuating miR172 mediated *Q* gene transcript degradation (Debernardi et al., 2017).

Cultivated soybean was believed to be domesticated from its wild progenitor *Glycine soja* in China 6,000–9,000 years ago and since then experienced substantial changes genetically and epigenetically (Ni et al., 2023; Sedivy et al., 2017; Shen et al., 2018; Wang et al., 2021a). For example, gene body DNA methylation differences are implicated in expression divergence between wild and cultivated soybeans (Kim et al., 2015). High-resolution Hi-C maps reveal that chromatin loop reorganization contributes to expression divergence of the genes during soybean domestication (Wang et al., 2021a). Besides, the comparison between wild soybeans, landraces, and cultivars detects extensive A/B compartment switching and TAD boundary variations, which are highly associated with presence and absence variation (PAV) (Ni et al., 2023). All of these studies suggest that epigenetic variations are involved in soybean domestication.

Heterosis

Heterosis refers to the superiority in hybrids over their parents concerning many traits like biomass, growth rate, yield, and so on. There are three classic genetic models for heterosis: dominance, overdominance, and epistasis (Figure 5A) (Birchler et al., 2010). The dominance model suggests that the dominant alleles from one parent can complement the deleterious recessive alleles from the other, thereby increasing the heterosis of the hybrids. The overdominance model suggests that heterosis is attributed to the superior interaction between the heterozygous genotypes compared with either parent's homozygous genotype. The epistasis model suggests that heterosis results from the interaction between non-allelic loci. All these three hypotheses focus on genetic factors and have been widely applied to population studies (Figure 5B). However, studies in the past decade have indicated that epigenetic regulations, including DNA methylation, histone modification, and chromatin organization, also have significant impacts in heterosis (Groszmann et al., 2013; He et al., 2013b; Kakoulidou and Johannes, 2024).

As a most stable and heritable epigenetic modification, DNA methylation between hybrids and their parents has been examined in several species, including Arabidopsis, rice, rapeseed, maize, pigeonpea, tomato, potato, and Chinese cabbage (Kakoulidou and Johannes, 2024; Ma et al., 2021). In Arabidopsis, an overall increase in DNA methylation in the hybrids compared with the parents has been reported (Kakoulidou and Johannes, 2024). Further studies showed that this methylation change, together with sRNAs, contributes to heterosis (Figure 5B) (Ariel et al., 2014; Greaves et al., 2012; Ma et al., 2021; Shen et al., 2012). For example, a comparative analysis of the *Ler* and C24 hybrids revealed that an increase in DNA methylation mainly occurred in regions displaying differential DNA methylation between the parents and was associated with increased levels of siRNAs. Consistent with this, RdDM is required for the establishment of both trans-chromosomal methylation (TCM) and trans-chromosomal demethylation (TCdM) in Arabidopsis (Figure 5B) (Kakoulidou and Johannes, 2024; Kawanabe et al., 2016; Li et al., 2023e; Zhang et al., 2016a; Zhang et al., 2016b). Inhibition of DNA methylation with 5′-Aza-dC treatment or abolishing the production of functional small RNAs by knocking out HEN1, an RNA methyltransferase, compromised heterosis (Shen et al., 2012). The circadian clock gene *CCA1* (*Central Circadian Oscillator 1*) was known to regulate plant hybrid vigor. The expression amplitudes of *CCA1* are influenced by the mCHH level in the promoter with a parent-of-origin effect, leading to the biomass heterosis in the hybrids. In the hybrids carrying mutations in RdDM, including *ago4* and *nprd1a*, the direction of the rhythmic expression of *CCA1* and hybrid vigor is reversed in reciprocal F1 crosses, further suggesting the significance of RdDM in heterosis (Ng et al., 2014).

In addition to Arabidopsis, heterosis, as an efficacious method of increasing yields, has been intensively studied in various crops and vegetables (He et al., 2013a; He et al., 2010; Li et al., 2021b;

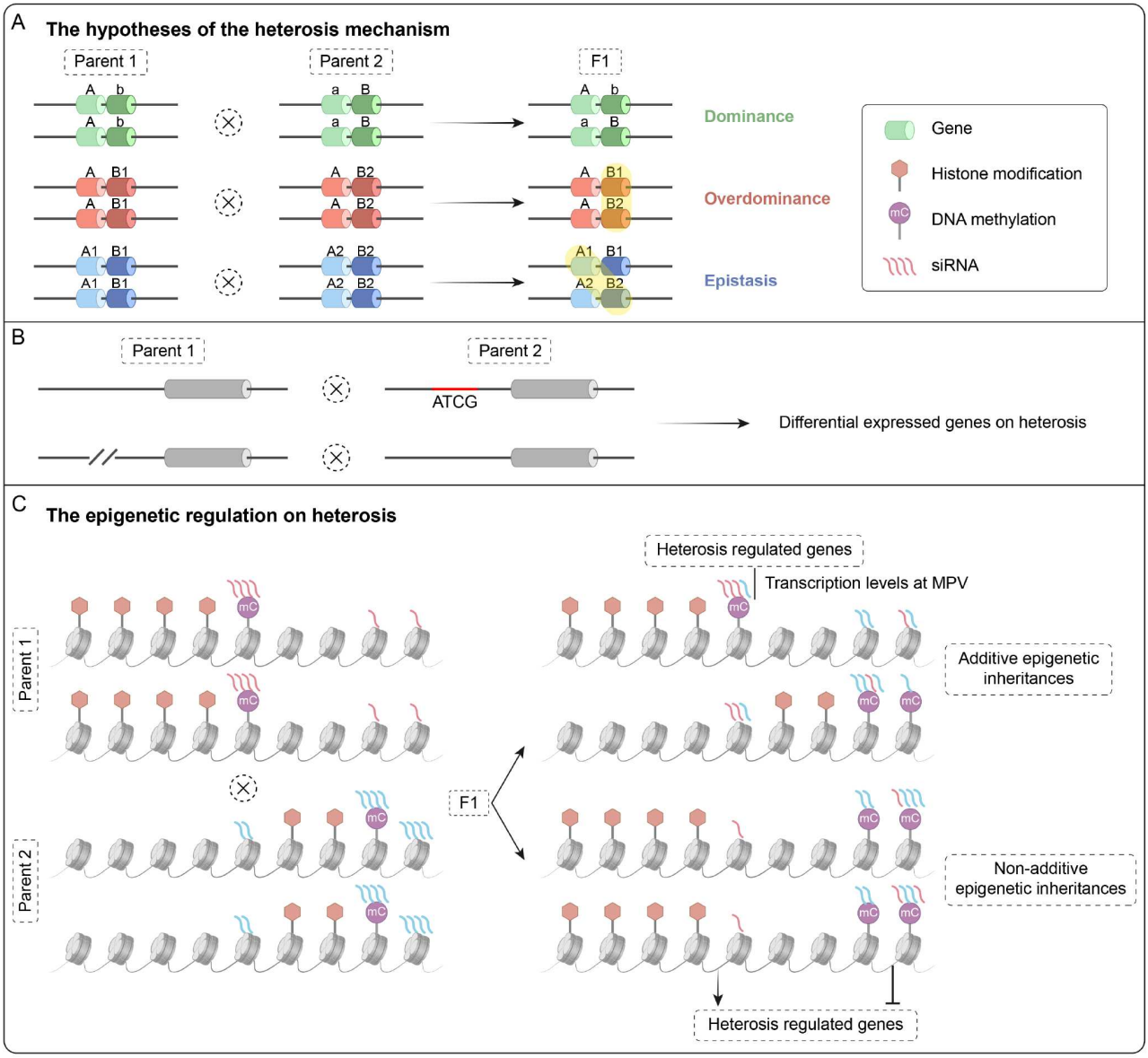

Figure 5. The molecular mechanism and epigenetic regulation of heterosis in plants. A, The three traditional hypotheses of heterosis including dominance, overdominance, and epistasis. B, Genome-wide differential gene expression of hybrids contributes to heterosis, which is correlated to InDels and SNPs of genic and promoter regions. C, The epigenetic regulations of heterosis including the DNA methylation differences and the histone modification differences between parents and hybrids. These regions with DNA methylation differences or histone modification differences in F1 hybrids affect the differential expression of genes related to heterosis. The increase of DNA methylation in hybrids, accompanied by an increase of siRNA, reveals that RdDM pathway may be involved in the regulation of heterosis.

Ma et al., 2021; Nakamura and Hosaka, 2009; Shivaprasad et al., 2012b). In rice, a comprehensive comparison between Nipponbare and 9311 revealed that sRNAs and DNA methylation were also involved in the differential expression of genes in the hybrids (He et al., 2010). In addition, most of the allelic-specific expression (ASE) in hybrids of ZS97 and MH63 was associated with mCHG. In maize, the hybrids showed a global decrease in 24-nt siRNA compared with the parents (Barber et al., 2012). In mung beans, most of the differentially expressed genes between the hybrids and parents exhibited differential DNA methylation, indicating a potentially significant role in heterosis (Junaid et al., 2018; Sinha et al., 2020). Interestingly, by comparing the level of CG DMRs between the parents and hybrids, it was reported that the exon CG DMRs were negatively correlated with the level of heterosis, while the TSS CG DMRs were positively correlated. Therefore, the ratio of CG DMR^{exon}/DMR^{TSS} may be a potential indicator to predict the level of heterosis in the hybrids. This hypothesis has been validated in 25 widely used rice parents and their hybrid offsprings (Fu et al., 2023a). In summary, the relationship between differential DNA methylation and heterosis associated gene expression has been widely reported, despite of varied degrees and scales (Figure 5C).

In some specific hybrids of Arabidopsis, no significant global changes in DNA methylation have been observed, such as in the hybrids of Col and C24 (Banaei Moghaddam et al., 2009; Banaei Moghaddam et al., 2011), Col and *Ler* (Dong et al., 2012), *Ler* and C24 (Zhu et al., 2017a). However, changes in histone modifications and gene expression occurred at specific loci, such as *FLC* (Figure 5C) (Zhu et al., 2017a). In a study with Col and C24 hybrids, the parental differences in H3K27me3 level are

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positively correlated with the allelic bias of H3K27me3 in the hybrids and thus, exhibiting ASE (Yang et al., 2015). Similarly in the rice hybrid of Nipponbare and 9311, a positive correlation between H3K4me3 and ASE has been reported, suggesting a conserved role of histone modification and heterosis (He et al., 2010). In Arabidopsis, histone H3 acetylation of key salicylic acid biosynthesis genes increases in hybrids and contributes to heterosis for bacterial resistance (Yang et al., 2015). Furthermore, histone modification rhythm alterations of *CCA1* play a role in eliminating the immunity-growth heterosis trade-offs in hybrids (Yang et al., 2021).

Recent research has suggested the role of 3D chromatin structure in heterosis. For example, in the hybrids of *Arabidopsis thaliana* and *Arabidopsis lyrata*, the chromatin from *A. thaliana* becomes more compact, while that from *A. lyrata* becomes decondensed (Zhu et al., 2017b). Additionally, hybrids displaying heterosis had more distal interactions among CD boundaries, loops, and homo-trans interactions compared with their parents. These interactions were mainly enriched in the promoters, leading to the modulation of genes in heterosis (Gao et al., 2024). In *Brassica napus*, analysis of the hybrids between FO and JM (displaying heterosis) and those between FV and JX (displaying no heterosis) suggests that the active A component had an enrichment of differentially expressed genes related to heterosis (Hu et al., 2022b). While the abovementioned studies shed light on the involvement of epigenetic modifications in heterosis, further studies are required to uncover the underlying molecular mechanisms.

Epigenome engineering

The fundamental principle of precise epigenome engineering is to target a chromatin modifying component to a specific locus in the genome, allowing gene expression to be regulated without altering the genome sequence (Miglani and Singh, 2020). This can be achieved through modulating various epigenetic components including DNA methylation, histone modification, or ncRNAs. Notably, DNA methylation exhibits a greater heritability (Quadrana and Colot, 2016; Yang et al., 2022d). Currently, artificial zinc finger (ZF)- and CRISPR-based technologies have been used for targeted epigenome engineering (Gallego-Bartolomé, 2020; Gardiner et al., 2022).

Zinc finger protein-based epigenome engineering

Cys2-His2 (C2H2) ZF domain is one of the most common nucleic acid binding domains in eukaryotes (Pabo et al., 2001). A single C2H2 ZF domain is formed by approximately 30 amino acids to recognize 3 nucleotides. Therefore, longer DNA sequences can be recognized by covalently concatenating multiple designed ZF domains (Pabo et al., 2001). Using a ZF protein with binding specificity towards the Arabidopsis *FWA* promoter (ZF108), a number of epigenetic regulators have been tested and shown to induce locus specific DNA methylation, gene silencing, and early flowering. These epigenetic regulators include SUVH2, DRM2, DMS3 Microrchidia (MORC), MOM1 (Gallego-Bartolomé et al., 2019; Johnson et al., 2014; Li et al., 2023d; Xue et al., 2021b). These studies suggest that specific targeting of DNA methylation components could be promising for heritable epigenome engineering (Figure 6A). Therefore, ZF-DMS3 have been utilized for epigenetic engineering in cassava (*Manihot esculenta*), a crucial carbohydrate source in tropical regions (Veley et al., 2023). *Xanthomonas phaseoli* pv. *manihotis* (*Xam*) is a bacterial pathogen that causes cassava bacterial blight. *Xam* secretes transcription activator-like20 (TAL20) into cassava cells to activate *MeSWEET10a* expression by binding to the Effector Binding Element (EBE) in its promoter. Directed methylation of EBE by ZF-DMS3 blocks the binding of TAL20, preventing the activation of *MeSWEET10a*, and thus increases resistance (Veley et al., 2023).

Similarly, to remove DNA methylation, the catalytic domain of human ten-eleven translocation (TET1cd) family DNA dioxygenases has been fused to ZF108 and proven to be effective in demethylating *FWA* (Zhang et al., 2018b; Gallego-Bartolomé et al., 2018). In addition, targeting TET1cd to a heterochromatic TE, *CACTA1*, also results in the loss of methylation. However, in contrast to *FWA*, *CACTA1* methylation was restored in the absence of the transgene (Gallego-Bartolomé et al., 2018).

Besides DNA methylation, histone modifications could also serve as the effectors in epigenome editing. A systematic screening of 270 putative chromatin proteins was conducted and those involved in H3K27me3 deposition (MSI1 and LHP1), H3K4me3 demethylation (JMJ14/18), and histone deacetylation (HD2A/B/C and HDA6) were able to silence *fwa-4* epiallele (Wang et al., 2023b). However, the repression is not heritable in the absence of the transgenes (Wang et al., 2023b).

CRISPR/dCas9-based epigenome engineering

Compared with the ZF strategy, deactivated Cas9 nuclease (dCas9) can recruit epigenetic effectors to genome with greater versatility (Gardiner et al., 2022; Thakore et al., 2016). To amplify the modifying effects, the SunTag system was utilized, where the tandem GCN4 peptide repeats were fused to dCas9, allowing the recruitment of multiple epigenetic modifiers (Figure 6B) (Tanenbaum et al., 2014). SunTag-TET1cd targeting *FWA* has been shown to generate heritable DNA demethylation (Gallego-Bartolomé et al., 2018). Similarly, SunTag-DRM2cd has been targeted to *FWA*, which triggered heritable DNA methylation (Papikian et al., 2019). In addition, a variant of bacteria-derived CG-specific DNA methyltransferase, MQ1 (SssI from *Mollicutes spiroplasma*), has been utilized to induce highly specific and heritable DNA methylation when tethered to ZF and CRISPR/dCas9 (Ghoshal et al., 2021). Recently, SunTag-MQ1 has been used to successfully methylate *miR157a* in Arabidopsis (Liu and Zhong, 2024).

To address the solubility issue of scFv in SunTag, MoonTag, which uses a nanobody NbGP41 and GP41 peptide pair, has been developed (Figure 6B) (Casas-Mollano et al., 2023). More recently, instead of using a single effector for DNA methylation or histone modification, a modular combinatorial epigenome editing platform, named SSSavi, has been developed (Swain et al., 2024). This system utilizes four different tags including SpyTag, SnoopTag, SunTag, and AviTag, which are fused to dCas9 to enable simultaneous recruitment of different effectors for editing DNA methylation, histone modifications, etc. (Swain et al., 2024). This modular multi-effector platform has been proven effective in human cells, but its application in plants and crops is yet to be investigated.

Other epigenome engineering methods

In addition to the abovementioned methods, a recent study

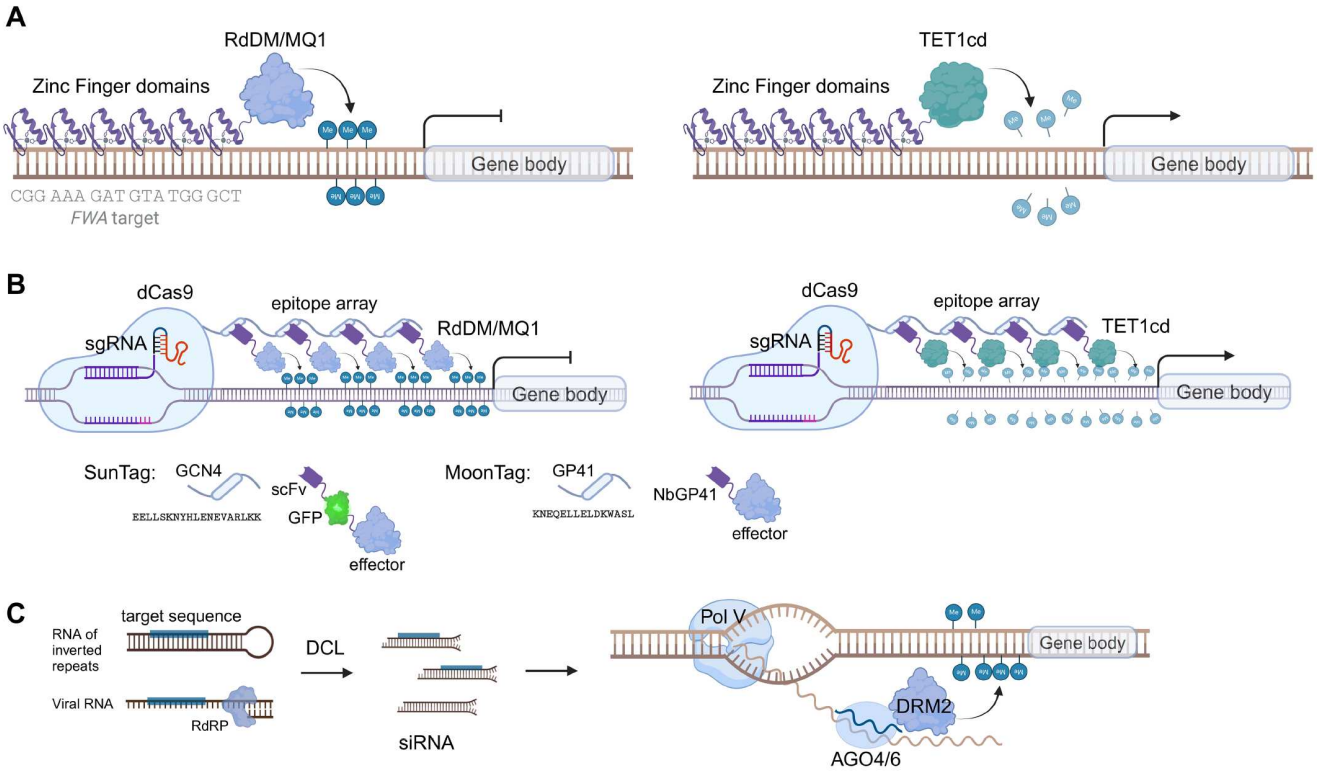

Figure 6. Tools for targeted DNA methylation engineering in plants. A and B, Zinc finger (A) and CRISPR/dCas9-based SunTag and MoonTag (B) can target effector proteins to specific loci in the genome. The effector can be RdDM components or the bacterial CG-specific DNA methyltransferase MQ1 for DNA methylation, or the catalytic domain of TET1 for DNA demethylation. In (A), each zinc finger domain recognizes three base pairs, and the *FWA* sequence is an example. In (B), the SunTag system and MoonTag system are similar, except that they use different epitope-antibody pairs. C, Targeting DNA methylation through the small RNA-based RdDM pathway. Expression of double-stranded RNA targeting a specific locus, through inverted repeats or virus-induced gene silencing, could generate siRNAs via DCL. The siRNA enters the RdDM pathway to establish DNA methylation.

showed that by depositing centromeric CEN180 repeats through CRISPR/Cas9-mediated knock-in, a local repressive chromatin environment with DNA methylation and H3K9me2 can be established (Liu et al., 2023e). The repressive marks could spread to flanking regions when IBM1 is absent, leading to heritable gene silencing lasting for at least five generations even without CEN180 repeats (Liu et al., 2023e). Another study showed that the insertion of 171 bp of human repetitive α-satellite DNA (alphoid DNA) could induce DNA methylation and H3K9me2 in tobacco cells (Otake et al., 2023). In addition, small RNAs have also been utilized for target specific deposition of DNA methylation and gene silencing (Figure 6C) (Bond and Baulcombe, 2015; Gallego-Bartolomé, 2020). These tools offer diverse epigenetic strategies for targeted gene regulation. In the future, it would be valuable to investigate the potential applications of this technique for crop enhancement.

Bioinformatic tools and resources for studying epigenetics

The advances in omics technologies made it possible for us to investigate epigenetic regulations at whole-genome level. Ample efforts have been made in developing more robust computational models for the efficient utilization of these multi-omics data. The list of commonly used computational tools has been provided at the following website (https://epigenie.com/epigenetic-tools-and-databases/). In addition, to characterize cell type-specific function of epigenetic regulators, tools that can perform quantitative comparisons of ChIP-seq data between multiple samples were developed, including MAnorm and MAmotif (Shao et al., 2012; Sun et al., 2018). Using MAnorm, specific roles of individual Polycomb complex components in different biological processes were elucidated, which include nutrient perception, development, and stress responses (International Wheat Genome Sequencing Consortium, 2018; Liu et al., 2019a; Wang et al., 2016; Ye et al., 2022; Zhou et al., 2018b).

The online platform, Plant-Regulomics (Ran et al., 2020; Sun et al., 2018), has collected and curated tens of thousands of transcriptomic and epigenomic data sets, and integrated a great variety of experimental pieces of evidence from multiple plant species. Using this platform, both up- and downstream regulators of a single gene, gene lists, or a specific genomic locus can be predicated with high confidence.

Perspectives

Our understanding of epigenetic regulations in diverse biological processes has progressed dramatically in the past decades. This knowledge offers us new strategies and tools for utilizing epigenetic regulations as a means for crop improvements. Compared with genetic variations, introducing epigenetic variations into crop improvements is advantageous as it does not involve changes in the genetic information of an organism and therefore may be more readily accepted by the public.

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However, there are challenges that need to be addressed before transforming epigenetic variations into useful breeding resources. Pleiotropic effects on plant development caused by global changes in the epigenetic landscape is often the case when key epigenetic regulators, such as DNA methyltransferases and histone modifiers, are mutated. Therefore, the identification of epi-alleles associated with beneficial traits will help provide useful targets. Compared with Arabidopsis, most crop plants have much larger genomes that contain higher contents of repetitive elements. Many more genes in these crop genomes have repetitive elements in or near them, and thus their expression is more likely influenced by the status of DNA methylation and associated chromatin modifications on the repetitive elements (Zhang et al., 2018b). Consequently, epialleles are likely more common in crop plants. Currently, the number of epi-alleles of useful breeding potential is still far from sufficient. Much effort is needed in the future to profile the complex epigenomes of crops.

An essential area in future is the tissue and cell type-specific epigenetic regulation. For instance, understanding how the components of the epigenetic regulatory complex are differentially assembled across various tissues and cell types, and how the assembly is determined by or responds to developmental and environmental stimuli, is crucial. Gaining this knowledge can significantly contribute to epigenetic engineering, particularly in targeting specific plant traits for enhancement in designated tissues, thus achieving an optimal balance among various developmental aspects. Consequently, elucidating the epigenetic regulatory mechanisms at the single-cell level is a pivotal research avenue.

Moreover, the establishment and reconfiguration of transgenerational epigenetic memory, and its influence on plant adaptation and evolution, are of significant interest. The emergence and stabilization of epigenetic variations may augment genetic diversity, aiding in plant adaptation, such as the diversification of traits among different crop cultivars. Population-level epigenome-wide association studies (EWAS), involving a substantial number of crop cultivars of differential breeding histories, could potentially identify and clarify this phenomenon if it exists.

In the context of agricultural application, stable heritability, both mitotically and meiotically, has to be achieved in the absence of the transgenic editing system. This remains a main challenge, especially with histone or chromatin modifications, which often are reset through cell divisions after the removal of the editing system. DNA methylation editing may or may not be heritable, depending on the genetic sequence as well as the type and extent of the editing. Success in maintaining the heritability of these modifications would be key to the utility of those epigenetically regulated traits. Therefore, strategies and tools that can enhance the heritability of epigenetic modifications are highly desirable.

Recent advances in targeted epigenetic modifications have further made precise editing possible. Still, on-target efficiency and specificity of the editing systems need to be improved. This is of particular importance considering that off-target editing may bring unwanted phenotypes.

Efficient epigenetic engineering as a breeding tool relies on successfully obtaining positive regenerants, which require efficient transgene delivery and plant regeneration. So far, agrobacteria mediated transgene delivery is still the most widely used method. Novel tools using agrobacteria independent gene delivery will further expand genetic engineering into plants and cultivars that are resistant to agrobacteria infection. However, the regeneration efficiency through traditional tissue culture remains extremely low for most cultivars of major crops. The genotype dependency of regeneration efficiency is a more common problem in obligate outcross crops of high genome heterozygosity. Therefore, understanding of the epigenetic mechanism in maintaining cell pluripotency and governing cell fate transitioning during plant regeneration would be of tremendous value. Particularly, characterization of the commonality and uniqueness of these epigenetic mechanisms across different plant species will for sure benefit the transformation efficiency regardless of the crop species.

In summary, further understanding of the epigenetic regulations in gene expression at the tissue and single cell levels; their roles in growth, development, and environmental interactions; identification of natural epigenetic variations during evolution and their contribution to phenotypic diversity and heterosis; as well as technologies that enable efficient translation of this knowledge into agricultural applications are needed.

Compliance and ethics

The authors declare that they have no conflict of interest.

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