Journal of Zhejiang University-SCIENCE B (Biomedicine & Biotechnology) *in press*
www.jzus.zju.edu.cn; www.springer.com/journal/11585
E-mail: jzus_b@zju.edu.cn

Review

https://doi.org/10.1631/jzus.B2500599

Dynamic DNA methylation landscapes in plants from the whole genome aspect: characteristics and future perspectives

Yurong HU, Wanmu ZHOU, Hui LU, Jiayan WU, Qinjie CHU✉

Institute of Crop Science, Zhejiang University, Hangzhou 310058, China

Abstract: DNA methylation, an important epigenetic modification, has been confirmed to act as an important regulator of gene expression and genome stability in plants. This review aimed to analyze DNA methylation landscapes in plants by integrating genome-wide DNA methylation data from 105 plant species, among which 53 species possess quantitative methylation levels for downstream analyses. We found that the levels of DNA methylation in plants are both interspecific and tissue-specific. Environmental stresses and evolutionary processes such as polyploidization, domestication and de-domestication can influence DNA methylation levels at the whole-genome level and single-gene level, respectively. Finally, we reviewed functional genes related to DNA methylation changes and highlighted the recent technological advances in multi-omics (e.g., scBS-seq, transcriptome, 3D chromatin architecture) for an improved interpretation of DNA methylation dynamics among plants and for environmental adaptation.

Key words: DNA methylation; Whole-genome bisulfite sequencing (WGBS); Tissue specificity; Stress treatment; Evolution

Unedited

1 Introduction

DNA methylation, as the most extensively studied epigenetic modification in plants, dynamically regulates gene expression and genome stability by silencing transposable elements and stabilizing chromosomal structure (Ruden et al., 2003; Duan et al., 2018; Yung et al., 2024). Following DNA replication, methylation is established or maintained by DNA methyltransferases (DNMTs) that move a methyl group from S-adenosylmethionine (SAM) to cytosine residues, primarily forming 5-methylcytosine (5-mC) but also, to a lesser extent, N^6-methyladenine (N^6-mA) and 7-methylguanine (7-mG) (Moore et al., 2013). 5-mC occurs in three sequence contexts—CG, CHG and CHH (where H = A, T or C)—each governed by a distinct enzymatic machinery in plants. Methyltransferase 1 (MET1) is mainly responsible for maintaining CG methylation in the coding regions of genes. The maintenance of CHG methylation in *Arabidopsis* is catalyzed mainly by the DNA methyltransferases CMT3 (Chromomethylase3) and CMT2 (Lindroth et al., 2001; Stroud et al., 2014), whereas CHH methylation is maintained through two major pathways: the RNA-directed DNA methylation (RdDM) pathway mediated by domains rearranged methyltransferase 2 (DRM2) and a CMT2-dependent pathway involving histone H3K9 methylation in heterochromatin (Chan et al., 2005; Law and Jacobsen, 2010; Zhang et al., 2018b). The spatiotemporal distribution of 5-mC arises from a dynamic equilibrium among de novo methylation, maintenance methylation, and active demethylation (Tan et al., 2016), thereby precisely regulating

✉ Qinjie CHU, qinjiechu@zju.edu.cn
Qinjie CHU, https://orcid.org/0000-0003-1234-3396
Yurong HU, https://orcid.org/0009-0005-7948-6393

Received Sept. 18, 2025; Revision accepted Dec. 24, 2025;
Crosschecked xxx. xx, 20xx; Published online xxx. xx, 20xx

© Zhejiang University Press 2026

developmental transitions, environmental stress responses, and genome integrity (Ibarra et al., 2012; He et al., 2022).

The emergence of whole-genome DNA methylation profiling technologies has transformed plant epigenetics research. In 2006, *Arabidopsis thaliana* became the first plant species to be subjected to comprehensive genome-wide methylation analysis, revealing its methylome landscape (Zhang et al., 2006). This pioneering study of *A. thaliana* demonstrated that gene body methylation correlates with constitutively high expression, whereas promoter methylation associates with tissue-specific transcriptional repression, substantially advancing our understanding of the global coordination of methylation and gene regulation (Zhang, et al., 2006). Over the past two decades, several methods have been derived for genome-wide DNA methylation mapping, including methylation sensitive amplification polymorphism (MSAP) (Francischini et al., 2017), high performance liquid chromatography (HPLC) (Chang et al., 2021), whole-genome bisulfite sequencing (WGBS) (Lister et al., 2009), methylated DNA immunoprecipitation sequencing (MeDIP-seq) (Ben Maamar et al., 2021), and reduced representation bisulfite sequencing (RRBS) (Meissner et al., 2005). Early approaches such as MSAP and HPLC provided initial insights into locus-specific or global methylation levels (Francischini, et al., 2017; Chang, et al., 2021). Subsequently, WGBS and MeDIP-seq enabled genome-scale profiling by converting unmethylated cytosine to uracil (Barros-Silva et al., 2018) and the specific enrichment of the 5'-methylcytosine antibody (Li et al., 2015), respectively. WGBS, currently regarded as the gold standard, achieves single-nucleotide resolution through bisulfite-mediated conversion of unmethylated cytosines to uracil (Saini et al., 2023). RRBS targets CpG-rich regions by MspI digestion (recognizing the CCGG motif) for cost-effective analysis (Nakabayashi et al., 2023). Nevertheless, each technique has their inherent limitations: MSAP and HPLC offer only low-resolution or global estimates, lacking base-resolution and locus specificity (Lisanti et al., 2013); WGBS is expensive and prone to bisulfite-induced artifacts and GC bias (Olova et al., 2018); MeDIP-seq suffers from antibody affinity bias and lower resolution (Weber et al., 2005); whereas RRBS is cost-effective but restricted to CpG-rich regions, leading to incomplete genome coverage (Gu et al., 2011).

In 2024, a systematic review of 456 published studies revealed that genome-wide methylome sequencing had been performed in 105 plant species (Fig. S1a, Table S1), encompassing major taxonomic groups such as grasses (17 species, 16.2%), legumes (10 species, 9.5%), and crucifers (6 species, 5.7%). Although early efforts focused predominantly on model species such as *Arabidopis thaliana* and *Oryza sativa*, recent years have seen a marked rise in the methylome profiling of non-model and wild plants (Fig. 1a). A bibliometric analysis of publications from 2000 to 2024 further indicates that research on plant DNA methylation has primarily addressed physiological processes (e.g., flowering and seed development) and abiotic/biotic stress responses (e.g., drought, salinity, and pathogen defence), highlighting their central role in plant adaptation and development (Fig. S1b). Methodologically, the field has progressed from locus-specific or low-resolution techniques (e.g., MSAP and HPLC) to high-resolution, epigenome-wide approaches, with WGBS now routinely applied to genomes ranging from 102 Mb (*Utricularia gibba*) to 14.4 Gb (*Triticum aestivum*) (Figs. 1a and 1b). This expansion has been facilitated by advances in sequencing technologies and computational epigenomics, enabling the precise, base-resolution quantification of DNA methylation even in complex, gigabase-scale plant genomes.

Unedited

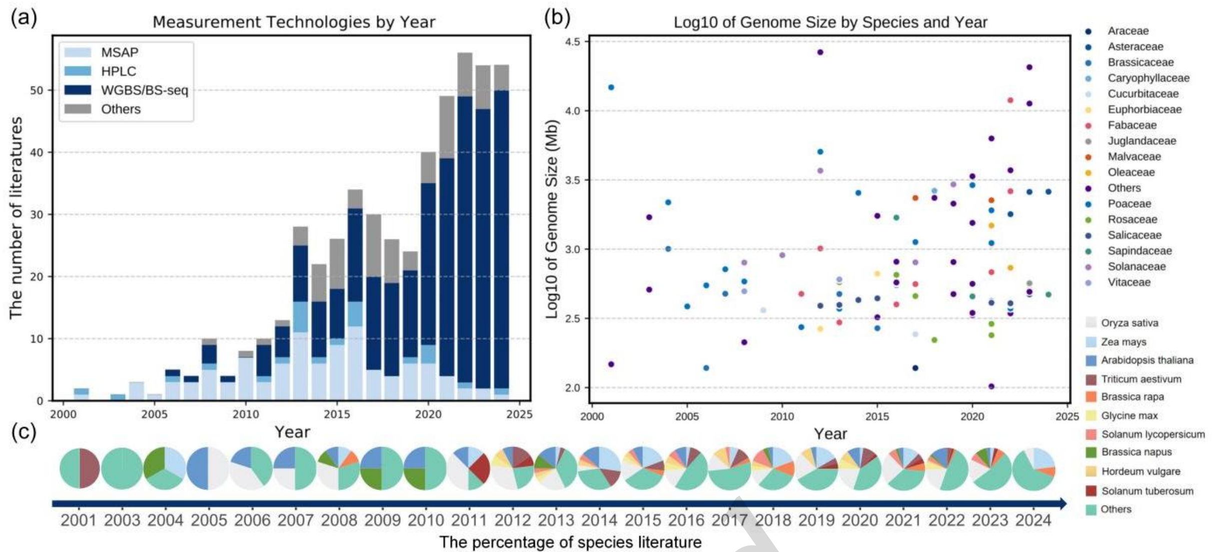


Fig. 1 Current status of DNA methylation research in plant species

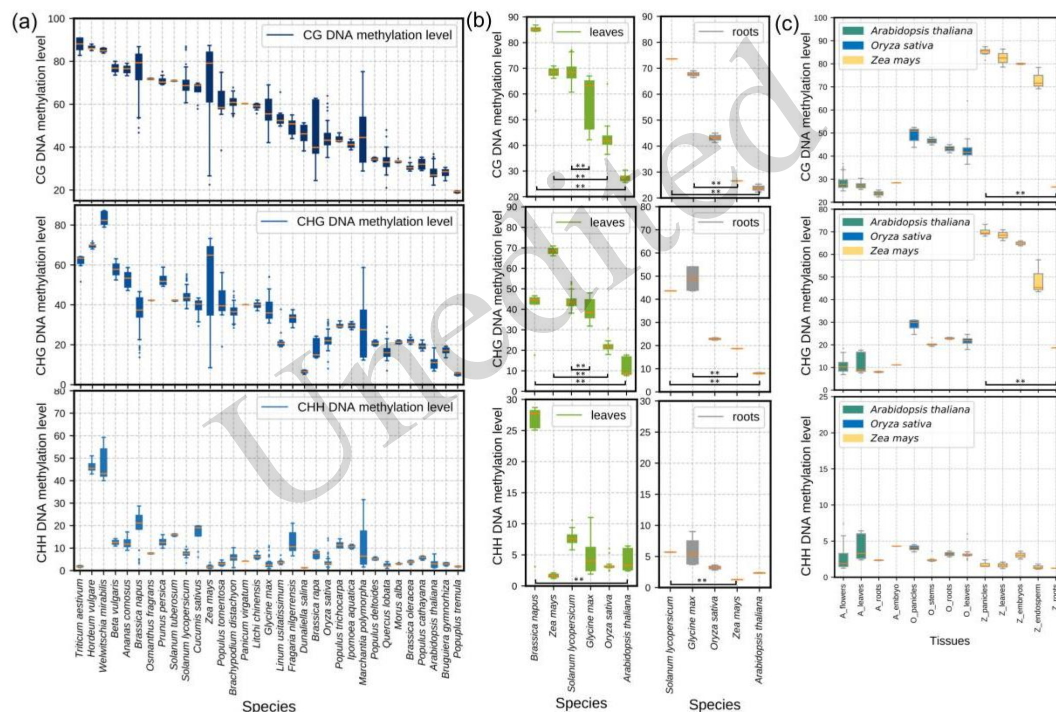
(a) Stacked graph showing the number of papers published using different DNA methylation sequencing technologies between 2001 and 2024. The x-axis tabulates the year and the y-axis indicates the number of documents. (b) Scatterplot showing the species and their genome sizes for which genome-wide DNA methylation studies were first performed between 2001 and 2024. Colors are assigned according to the family to which the species belongs. The x-axis indicates the year and the y-axis indicates genome size (taken as log10 in Mb). (c) Sector diagram showing the distribution of the major species in which DNA methylation studies were carried out during 2001-2024. MSAP, methylation sensitive amplification polymorphism; HPLC, high performance liquid chromatography; WGBS/BS-seq, whole-genome bisulfite sequencing/bisulfite sequencing.

Unedited

2 Interspecific divergence and tissue specificity of DNA methylation landscapes across plant species

DNA methylation exhibits marked interspecific variation across plant genomes, with methylation levels in higher-order plants ranging from 4.16% to 30% globally (Leutwiler et al., 1984). This variation is strongly context-dependent: in 96% of the 53 species with quantitative whole-genome methylation data, methylation follows the order mCG > mCHG > mCHH, with the sole exception being *Mikania micrantha* (mCG > mCHH > mCHG, Table S2). Across species, methylation levels range from 9.41% to 90.60%, 3.37% to 83.15%, and 0.97% to 47.62%, respectively. *Lactuca sativa* (*Asteraceae*) and *Welwitschia mirabilis* (*Welwitschiaceae*) display the highest CG and non-CG (CHG/CHH) methylation levels, respectively, whereas *Spirodela polyrhiza* (*Araceae*) shows the lowest DNA methylation values in all three contexts (Fig. S2). Among the 53 species surveyed, members of the *Poaceae* family exceed 50% methylation in CG and CHG contexts more frequently than species from other families. Within *Poaceae*, hexaploid bread wheat (*T. aestivum*; $2n$=$6x$=42, AABBDD, ~14.5 Gb) exhibits exceptionally high CG methylation (Fig. 2a), likely due to its large, repeat-rich genome ($2n$=$6x$=42, AABBDD, with a genome size of about 14.5 Gb) and its abundance of repetitive sequences, which make up 85% of the genome (Walkowiak et al., 2020). Notably, CHG methylation is sharply reduced in *Triticum durum* (tetraploid wheat, AABB) compared to *T. aestivum* (hexaploid wheat, AABBDD) (Yuan et al., 2020). However, even diploid grass progenitors (*Triticum monococcum*, *Triticum urartu*) and other diploid grasses (*O. sativa*, *Sorghum bicolor*) already show substantially higher methylation than most dicots (Niederhuth et al., 2016). This pattern is largely attributable to the massive expansion of Gypsy and Copia retrotransposons in grass genomes and the sustained activity of CMT3- and RdDM-dependent methylation pathways, rather than ploidy alone (Takuno et al., 2016). In wheat, polyploidisation appears to amplify this pre-existing tendency, possibly through genome-shock responses.

In terms of tissue specificity, DNA methylation in plants displays striking differences, with considerable variation both within and between species. Comparative analyses of six plants (*O. sativa*, *Zea mays*, *A. thaliana*, *Brassica napus*, *Glycine max*, and *Solanum lycopersicum*) revealed that *S. lycopersicum* and *B. napus* had the highest CG/CHH methylation values in root and leaf tissues, respectively, while *A. thaliana* presented the lowest in both tissues (Fig. 2b). As for CHG methylation, *G. max* displayed the highest levels in roots and *Z. mays* in leaves. Intraspecific comparisons further underscored the developmental plasticity of DNA methylation across tissues (Fig. 2c). For instance, compared with other tissues, panicles retained high CG / CHG methylation patterns in both *O. sativa* and *Z. mays*. The DNA methylation level of maize roots was significantly lower than that of other tissues. Interestingly, flower tissues of *A. thaliana* also displayed the highest CG methylation values, indicating the conservation of a high DNA methylation level of plant reproductive tissues compared with vegetative tissues.



Unedited

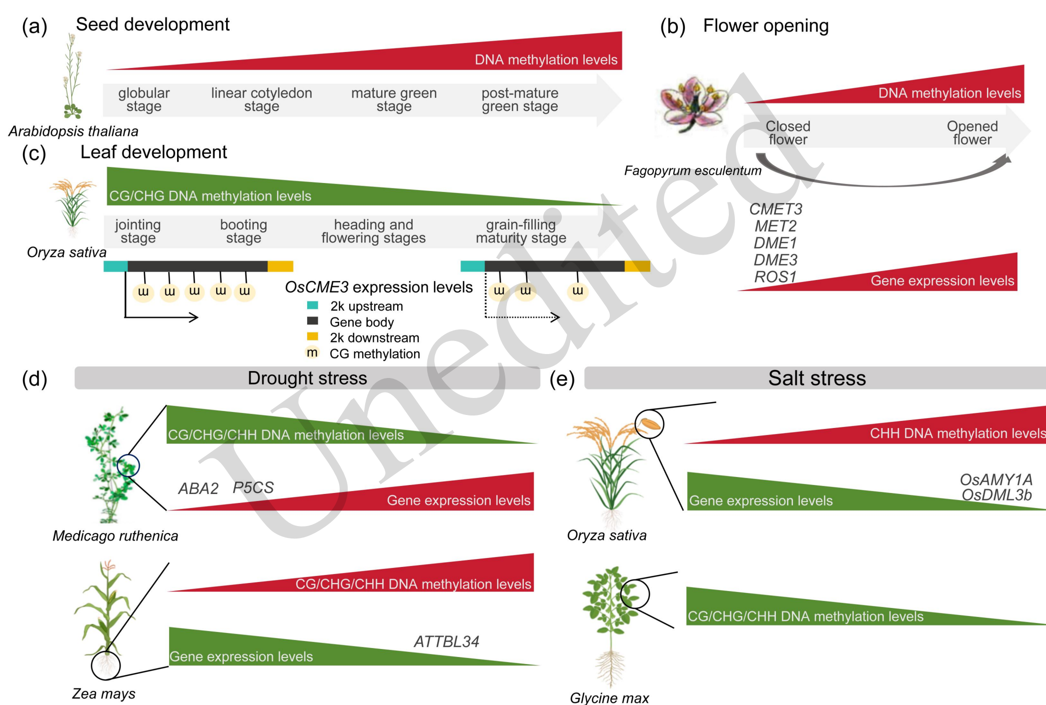
Fig. 2 Distribution of DNA methylation levels in plant species from multiple samples

(a) Distribution of DNA methylation values in 33 plant species based on multiple samples. The x-axis indicates the species name and the y-axis indicates the genome-wide CG/CHG/CHH DNA methylation level of that species. (b) Differences in CG/CHG/CHH DNA methylation levels in the roots of *S. lycopersicum*, *G. max*, *O. sativa*, *Z. mays*, and *A. thaliana*, and leaves of *B. napus*, *Z. mays*, *S. lycopersicum*, *G. max*, *O. sativa*, and *A. thaliana*. The x-axis denotes the name of the species and the y-axis denotes the corresponding CG/CHG/CHH DNA methylation levels. Significant differences are indicated by ** ($P<0.01$, Student's t-test). (c) Differences in CG/CHG/CHH DNA methylation levels in different tissues of *A. thaliana*, *O. sativa*, and *Z. mays*. Tissues: flower, leaf, root, stem, embryo, endosperm, and spike. The x-axis denotes the name of the tissue and the y-axis denotes the CG/CHG/CHH DNA methylation level.

3 Developmental dynamics of DNA methylation

DNA methylation serves as a master regulatory switch coordinating plant developmental transitions. For example, during *A. thaliana* seed development (Fig. 3a), DNA methylation levels of seeds increase from the globular stage to the mature green stage (Kawakatsu et al., 2017). For the flower opening of *Fagopyrum*

esculentum, the DNA methylation of nectaries of open flowers exhibit higher levels than that of closed flowers (Sala-Cholewa et al., 2024), and expression values of genes associated with DNA methylation (*MET1*, *MET2*, *CMET3*) and demethylation (*DME1*, *DME3*, *ROS1*) are downregulated (Fig. 3b). The genomic DNA methylation levels of moso bamboo increase with physiological age (Yuan et al., 2014). In addition, *Populus alba* exhibits an overall trend toward hypermethylation during spring growth and hypomethylation during winter hibernation during spring growth and winter hibernation, respectively (Guarino et al., 2015). However, the DNA methylation levels also present a strong spectrum of fluctuations throughout the seed development of *O. sativa*, with the highest values observed at 6 DAP in *O. sativa ssp. indica* and at 2 DAP in *O. sativa ssp. japonica* (Xing et al., 2015). In contrast, the CG methylation of leaves decreases globally during the four stages of *O. sativa* development (Fig. 3c), with the reduction of CG methylation in the gene body of *OsCME3*, which plays a crucial role in leaf horn development (Zhou et al., 2024).



Unedited

Fig. 3 Dynamics of DNA methylation during plant development and under abiotic stress

(a) Dynamics of DNA methylation levels during A. thaliana seed development. (b) Dynamics of DNA methylation levels in F. esculentum flowers (nectaries) from closed to developed state. (c) Dynamics of DNA methylation in leaves during four periods of O. sativa development, from the jointing stage, to the booting stage, to the heading and flowering stages to the grain-filling maturity stage. (d) DNA methylation changes of drought-resistant Z. mays and Medicago ruthenica under drought stress. (e) DNA methylation changes of salt-sensitive O. sativa IR29 and G. max C08 under salt stress.

4 DNA methylation patterns in plants under biotic and abiotic stresses

The epigenetic regulation of plants in the face of adverse stresses is primarily mediated by biotic and abiotic stresses (Boyko and Kovalchuk, 2011). Plants respond to stress by silencing or activating stress-responsive genes through DNA methylation and demethylation, thereby adapting to harsh environments (Deleris et al., 2016). To this end, different species exhibit distinct DNA methylation dynamics in response to stress treatments (Table 1).

Table 1 Whole-genome and gene changes of DNA methylation in plants responding to biotic and abiotic stresses

Stress		Whole-genome changes		Gene changes	
		Increased	**Decreased**	**Increased**	**Decreased**
Biotic	Virus infection	tobacco (Wang *et al.*, 2024)	/	/	/
Abiotic	Drought	*Populus trichocarpa* (leaf) (Liang et al., 2014) *Sesamum indicum* (leaf) (Feng et al., 2010)	/	drought resistance genes (*O. sativa*) (Xu et al., 2021)	/
	Salt	*Chloris virgata* (root) (Cao et al., 2012) *Medicago sativa* (Rosellini et al., 2016) *O. sativa* (leaf, CHH) (Li and Guo, 2023)	*Solanum tuberosum* (Ai et al., 2021) *G. max* (seedling) (Chen et al., 2019)	/	*OsDML3b* (*O. sativa*) (Li and Guo, 2023)
	Low-temperature	/	*Cucumis sativus* (leaf) (Wang et al., 2023b)	/	/
	Heavy metal	*B. napus* (Filek et al., 2008) *Raphanus sativus* (Yang et al., 2007)	/	/	/
		/	*Trifolium repens* (Ding et al., 2014) *Cannabis sativa* (Ding, et al., 2014)	/	/

Unedited

For example, under biotic stress, tobacco mosaic virus infection increases genomic DNA methylation levels in Nicotiana tabacum while reducing methylation in leucine-rich repeat sequences associated with disease resistance (Wang et al., 2024). Under abiotic stress, drought elevates DNA methylation levels in Populus trichocarpa (Liang, et al., 2014) and Sesamum indicum (Feng, et al., 2010), as well as in drought-resistance genes of O. sativa (Xu, et al., 2021). Meanwhile, salt stress induces a decrease in the total level of DNA methylation in S. tuberosum (Ai, et al., 2021) and an increase in the total level of DNA methylation in M. sativa (Al-Lawati et al., 2016), where the DNA methylase OsDML3b is significantly downregulated under salt stress and the level of CHH methylation is significantly elevated in rice IR29 (Li and Guo, 2023). Salt stress also triggers a decrease in DNA methyltransferase activity in the leaves of G. max seedlings (Chen, et al., 2019), resulting in genome-wide hypomethylation that may enhance abscisic acid-dependent stress responses through the key transcription factors ABA2 and P5CS (Yung, et al., 2024). Low-temperature stress progressively reduces DNA methylation levels in C. sativus leaves (Kumar et al., 2016; Wang, et al., 2023b). Heavy metal stress induces different trends in altering DNA methylation levels in plants (Giannelli et al., 2024), where Cd2+ and Cr6+ treatments lead to an increase in genomic DNA methylation levels in B. napus (Filek, et al., 2008) and R. sativus (Yang, et al., 2007) but lead to a decrease in genomic DNA methylation levels in T. repens and C. sativa. While the changes in the methylation levels of relevant genes in Z. mays after Pb2+ treatment were both high and low (Ding, et al., 2014), there was also a dose effect in the alteration of genomic DNA methylation levels in O. sativa and T. aestivum treated with different concentrations of Cu2+, Cd2+ and Hg2+ (Kong et al., 2020). In addition, plants may experience long-term methylation changes after abiotic stress (Chen et al., 2022a), and these

changes can be “remembered” during the subsequent growth cycle and affect the plant's response to subsequent stresses (Quadrana and Colot, 2016).

5 Changes in DNA methylation levels during plant evolution

Over longer evolutionary timescales, species may undergo significant changes in genome-wide methylation levels (Wambui Mbichi et al., 2020). These changes are associated with several factors, including genome size, structural complexity and the number of transposons and repetitive sequences (Kenchanmane Raju et al., 2023).

DNA methylation serves as an important regulatory mechanism during plant evolution, including processes such as domestication and de-domestication, primarily via modulating the activity of transposons and repetitive sequences (Zhong, 2016). Gene duplication is a major source of evolutionary novelty, and DNA methylation can influence the fate of duplicated (paralogous) genes by affecting their expression (Kenchanmane Raju, et al., 2023). Studies exploring the relationship between DNA methylation and parallel evolution have revealed that methylation patterns differ according to repeat type, repeat age, sequence divergence, and gene expression levels (Feil and Berger, 2007).

It was found that, compared to diploid wheat *A. tauschii* (DD) and natural tetraploid wheat (NTW, AABB), the CG/CHG/CHH DNA methylation levels in the endosperm of natural hexaploid wheat (NHW, AABBDD) were increased (Yuan, et al., 2020). In hexaploid wheat, regions with high densities of differentially methylated regions (DMRs) were associated with elevated H3K9me2 levels and reduced expression of histone variant genes. These findings suggest synergistic epigenetic modifications following polyploidization, a pattern also observed during cotton polyploidization (Song et al., 2017). For polyploids, it was also found that the sub-genome dominant/balanced phenomenon of DNA methylation level was inherited from ancestors in *Echinochloa* species (Walkowiak, et al., 2020), wheat and cotton (Chu et al., 2025). On the other hand, the rate of change in DNA methylation exceeds that of neutral sequence substitutions during the evolution of cotton (Song, et al., 2017). It was also found that, during the evolution of peanut from diploid to tetraploid, CHG-type DNA methylation may be an important epigenetic modification mechanism for the differential expression of homologous genes (Li et al., 2023). During the domestication of rice from wild to cultivated rice, CG DNA methylation levels decreased significantly (Cao et al., 2023), which also occurred in the domestication process of *Echinochloa* species (Chu, et al., 2025). Notably, DNA methylation changes in different genomic regions by affecting chromatin accessibility, histone modification, transcription factor binding, and chromatin loop formation during the two opposite stages of rice domestication and de-domestication (Cao, et al., 2023). In addition, a study compared the level of methylation in three different sequence contexts (CG, CHG, and CHH) in the promoter region among haploid (1X), diploid (2X), and triploid (3X) seedlings, and found that relative levels of DNA methylation across different ploidy levels was in the order of diploid > triploid > haploid (Zhang et al., 2018a). The observed methylation changes may reflect regulatory responses to environmental conditions, potentially influencing gene expression and epigenetic memory, while their roles in adaptive evolution remain to be determined.

Beyond evolutionary patterns, DNA methylation is a highly dynamic process that plays a critical role in regulating gene expression in response to developmental and environmental cues. Hypermethylation in promoter regions is generally associated with transcriptional repression, whereas gene-body methylation (gbM) in actively transcribed genes is often positively correlated with expression levels, potentially by suppressing cryptic transcription or enhancing elongation efficiency (Bewick and Schmitz, 2017; Luo et al., 2018). Numerous studies have demonstrated that developmental transitions (e.g., seed germination, flowering) and abiotic/biotic stresses trigger the rapid reprogramming of methylation patterns that directly modulate stress-responsive or developmental genes. For instance, drought, salinity and cold stress frequently induce the hypermethylation of promoter regions in stress-responsive genes (e.g., RD29A, COR15A) leading to their

transcriptional repression under normal conditions, whereas demethylation under stress enables rapid activation (Wibowo et al., 2016). Conversely, loss of methylation in transposable elements near genes may increase expression variation or generate epialleles that affect phenotypic plasticity. Active DNA demethylation mediated by ROS1/DML family enzymes has also been shown to be essential for resetting methylation states and maintaining the proper expression of key developmental regulators (Gong et al., 2002; Lei et al., 2014).

6 Functional genes are influenced by DNA methylation

The altered methylation of promoter regions, exon regions, or gene body regions of functional genes in plants usually affects gene expression and produces specific phenotypes (Table 2).

Table 2 DNA methylation-related functional genes in *A. thaliana* and *O. sativa*

Species	Gene name	Description
A. thaliana	*RPT2a*	RPT2a promotes DNA METHYLTRANSFERASE1 degradation leading to DNA hypomethylation upstream of TFL1 (Yao et al., 2024)
A. thaliana	*FVE, FY, FLD, PEP, HDA5, FLC, PRP39-1*	FY, PEP, PRP39-1, FVE, FLD, FLC, and HDA5 are involved in RNA processing, transcription, post-transcription, and chromatin modification, and the expression levels are negatively correlated with CG methylation levels (Xie et al., 2024)
A. thaliana	*AtALKBH1A*	ALKBH1 is a DNA 6ma demethylase that effectively eliminates DNA 6ma methylation (Li et al., 2024)
A. thaliana	*AGDP3*	AGDP3 is a cytokine required to prevent gene silencing and DNA hypermethylation (Zhou et al., 2022)
A. thaliana	*ACD6, ACO3, GSTF14*	Abiotic stresses, including water deficit, cold and salt stress, induce demethylation of ACD6, ACO3 and GSTF14 promoter repeat sequences (Yang et al., 2022)
A. thaliana	*MEM1*	Upregulation of a group of DNA methylation pathway genes in mem1 mutants leads to elevated global DNA methylation levels (Wang et al., 2022b)
A. thaliana	*MET1*	MET1 inactivation is able to substantially reduce CG methylation (Srikant et al., 2022)
A. thaliana	*BPM1*	Overexpression of BPM1 leads to elevated methylation levels of two RdDM-regulated gene promoters, FWA and CML41, and CHH methylation levels (Jagić et al., 2022)
A. thaliana	*RLL5 -1*	RLL5, an f-box-containing protein, is involved in preventing transgene silencing and maintaining global DNA methylation in *A. thaliana* (Hou et al., 2022)
A. thaliana	*IDM3*	IDM3 is involved in the ROS1-mediated DNA demethylation pathway (Miao et al., 2021)

Unedited

A. thaliana	*ROS1*	ROS1-directed demethylation of the MG1 and RLP43 kinetochores affects both flagellin responsiveness and basal resistance (Halter et al., 2021)
A. thaliana	*FWA*	Cytosine methylation of the FWA promoter is part of a regulatory system that regulates callus regenerative capacity and direct in vitro shoot regeneration (Dai et al., 2021)
A. thaliana	*CFK1*	CFK1-mediated degradation of DRM2 protein leads to drm2-like DNA hypomethylation (Chen et al., 2021)
A. thaliana	*TCX5*	TCX5 is a transcriptional repressor of genes required to maintain DNA methylation (Ning et al., 2020)
A. thaliana	*Block C*	Inverted repeats of Block C induce localized DNA methylation and heterochromatin formation, leading to downregulation of FT in the induced photoperiod (Zicola et al., 2019)
A. thaliana	*AtICE1*	The expression levels of all members of the CBF pathway except the AtCBF2 gene were negatively correlated with the methylation level of the AtICE1 gene (Xie et al., 2019)
O. sativa	*OsAGO2*	OsAGO2 binds to 24-nt microRNA and to the promoter region of OsNAC300, leading to DNA methylation (Zheng et al., 2024)
O. sativa	*OsMYBX9*	The methylation levels of the promoter region (CHG) and exon region (CHH) of the negatively regulated gene OsMYBX9 negatively regulate its expression (Wang et al., 2023a)
O. sativa	*OsROS1a*	The rice genome contains four ROS1 paralogous genes (OsROS1a, OsROS1b, OsROS1c, and OsROS1d) that mediate DNA demethylation, and in the osros1a mutant, the CG and CHG methylation of the promoter of the OsPKS2 gene was significantly increased (Xu et al., 2022)
O. sativa	*OsRDR2*	Mutations in OsRDR2 eliminated the accumulation of 24-nt small interfering rna, thereby greatly reducing genome-wide CHH (H = A, C, or T) methylation (Wang et al., 2022a)
O. sativa	*NLR*	The rice NLR gene was severely methylated at the CG locus by 9311 and P427 at room and low temperatures (Chen et al., 2022b)
O. sativa	*IPA1*	Methylation of IPA1 promoter repeat sequences negatively regulates IPA1 expression at the transcriptional level (Zhang et al., 2017)
O. sativa	*MITE #1*	mit# 1 deletion leads to down-regulation of the D14 gene and increased tillering in rice (Arite et al., 2009; Xu et al., 2020)

RPT2a, REGULATORY PARTICLE AAA-ATPASE 2a; TFL1, TERMINAL FLOWER1; FY, FLOWERING LOCUS Y; PEP, PEPPER; PRP, 39-1PRE-MRNA PROCESSING PROTEIN 39-1; FVE, FLOWERING LOCUS VE; FLD, FLOWERING LOCUS D; FLC, FLOWERING LOCUS C; HDA5, HISTONE DEACETYLASE 5; ALKBH1A, ALKB HOMOLOG 1A; AGDP3, AGENET DOMAIN CONTAINING PROTEIN 3; ACD6, ACCELERATED CELL DEATH 6; ACO3, ACID OXIDASE 3; GSTF14, GLUTATHIONE S-TRANSFERASE 1; MEM1, METHYLATION ELEVATED MUTANT 1; MET1, METHYLTRANSFERASE 1; BPM1, MATH-BTB PROTEINS; RLL5 -1, REDUCED LUC LUMINESCENCE 5-1; IDM3, INCREASED DNA METHYLATION 3; ROS1, REPRESSOR OF SILENCING 1; RMG1, RESISTANCE METHYLATED GENE 1; RLP43, RECEPTOR-LIKE PROTEIN 43; FWA, FLOWERING WAGENINGEN; CFK1, COP9 INTERACTING F-BOX KELCH 1; TCX5, TSO1-LIKE CXC DOMAIN-CONTAINING PROTEIN 5; ICE1, INDUCER OF CBF EXPRESSION 1; AGO2, ARGONAUTE 2; MYBX9, MYELOBLASTOSIS X9; RDR2, RNA-DEPENDENT RNA POLYMERASE 2; NLR, NUCLEOTIDE-BINDING LEUCINE-RICH REPEAT; IPA1, IDEAL PLANT ARCHIECTURE; MITE #1, MINIATURE INVERTED-REPEAT TRANSPOSABLE ELEMENT #1.

Unedited

For example, in *A. thaliana*, *FY*, *PEP*, *PRP39-1*, *FVE*, *FLD*, *FLC*, and *HDA5* are involved in RNA processing, transcription, post-transcription, and chromatin modification, and the expression levels of these seven upstream genes are negatively correlated with genome-wide CG methylation levels (Xie, et al., 2024), potentially playing a role in regulating flowering time. Abiotic stresses such as water deficit, cold and salt stress can induce the demethylation of promoter repeat sequences of upstream regulators of the salicylic acid (SA) defense pathway, and then transcriptionally activate the expression of *ACD6* (Small proteins modulate ion-channel-like), *ACO3* (ABA pathway-related gene), and *GSTF14* (Glutathione s-transferase superfamily endogenous gene) (Yang, et al., 2022).

In *O. sativa*, the expression of rice tillering regulator *IPA1* is negatively regulated at the transcriptional level by the methylation of repetitive sequences in the *IPA1* promoter (Zhang, et al., 2017). The expression of *D14* is downregulated by the hypomethylation of miniature inverted-repeat transposable elements (MITEs) in the downstream region of itself, which is involved in gibberellin biosynthesis and signaling and results in an increase in rice tillering (Arite, et al., 2009; Xu, et al., 2020). Variation in the DNA methylation of lignin synthesis-related *OsSWN1*, *OsMYBX9*, *OsPAL1*, and *Os4CL3* mediated the differences in their expression levels and affected the ratio of cellulose to lignin content (Wang, et al., 2023a). Collectively, these examples underscore the need for deeper investigations into how regional DNA methylation changes regulate gene expression.

Unedited

7 Concluding remarks and future perspectives

This study compiled comparable genome-wide DNA methylation data from 105 plant species, with quantitative methylation levels available for a representative subset of 53 species, to examine plant DNA methylation patterns across species, tissues, environmental stresses, and evolutionary contexts. Our analyses revealed substantial variation in DNA methylation levels among plants, providing a valuable resource for understanding the regulatory roles of DNA methylation in plant biology. Future studies incorporating a broader range of species, tissue types and ecological conditions will be necessary to determine whether these observed methylation trends are generalizable across diverse plant lineages and biological contexts.

Advanced integrative multi-omics approaches that combine WGBS with RNA-seq, ChIP-seq, ATAC-seq, Hi-C, MeRIP-seq, and single-cell technologies are transforming plant DNA methylation research (Gu et al., 2024). DNA methylation and transcriptional reprogramming represent common stress responses in plants, mediated by transcription factors that recruit epigenetic regulators to remodel chromatin (Ouyang et al., 2020; Rimoldi et al., 2024). Evidence from A. thaliana and Z. mays shows that histone modifications and DNA methylation act dynamically during cell differentiation and stress adaptation, reverting once stress is relieved (Zhao et al., 2014; Yu et al., 2023). Novel tools such as ATAC-Me already enable the simultaneous profiling of chromatin accessibility and methylation (Zhu et al., 2023b), while Hi-C, combined with RNA-seq, ChIP-seq and WGBS, uncovers 3D chromatin-gene regulatory networks (Lieberman-Aiden et al., 2009; Burton et al., 2013; Zhu et al., 2023a). Emerging links between 5mC and RNA methylation (m6A) (Zhou et al., 2019), together with the recent adaptation of single-cell methylation profiling for plants (Tian et al., 2023), highlight the need for frameworks that connect DNA methylation to transcription factor networks, histone modifications, and 3D chromatin architecture as priority directions for future research.

Data availability statement

The data will be made available upon request.

Declaration on the Use of Generative AI Tools

No generative AI tools were used in the preparation of this manuscript.

Acknowledgments

The work was supported by Zhejiang Key Laboratory of Crop Germplasm Innovation and Utilization Open Fund; and the National Natural Science Foundation of China (32101729).

Author contributions

Yurong Hu: Data Curation, Visualization, Formal Analysis, Writing - Original Draft. Wanmu Zhou: Data Curation. Hui Lu: Data Curation. Jiayan Wu, Data Curation. Qinjie Chu: Conceptualization, Writing - Review & Editing, Supervision, Project administration, Funding acquisition. All authors read and approved the final manuscript and, therefore, had full access to all the data in the study and take responsibility for the integrity and security of the data.

Compliance with ethics guidelines

The authors declare no competing interests.

References

Ai Y, Jing S, Cheng Z, et al., 2021. DNA methylation affects photoperiodic tuberization in potato (solanum tuberosum l.) by mediating the expression of genes related to the photoperiod and ga pathways. *Hortic Res*, 8(1):181. https://doi.org/10.1038/s41438-021-00619-7

Al-Lawati A, Al-Bahry S, Victor R, et al., 2016. Salt stress alters DNA methylation levels in alfalfa (medicago spp). *Genet Mol Res*, 15(1):15018299. https://doi.org/10.4238/gmr.15018299

Arite T, Umehara M, Ishikawa S, et al., 2009. D14, a strigolactone-insensitive mutant of rice, shows an accelerated outgrowth of tillers. *Plant Cell Physiol*, 50(8):1416-1424. https://doi.org/10.1093/pcp/pcp091

Barros-Silva D, Marques CJ, Henrique R, et al., 2018. Profiling DNA methylation based on next-generation sequencing approaches: New insights and clinical applications. *Genes (Basel)*, 9(9) https://doi.org/10.3390/genes9090429

Ben Maamar M, Sadler-Riggleman I, Beck D, et al., 2021. Genome-wide mapping of DNA methylation 5mc by methylated DNA immunoprecipitation (medip)-sequencing. *Methods Mol Biol*, 2198:301-310. https://doi.org/10.1007/978-1-0716-0876-0_23

Bewick AJ, Schmitz RJ, 2017. Gene body DNA methylation in plants. *Curr Opin Plant Biol*, 36:103-110. https://doi.org/10.1016/j.pbi.2016.12.007

Boyko A, Kovalchuk I, 2011. Genome instability and epigenetic modification--heritable responses to environmental stress? *Curr Opin Plant Biol*, 14(3):260-266. https://doi.org/10.1016/j.pbi.2011.03.003

Burton JN, Adey A, Patwardhan RP, et al., 2013. Chromosome-scale scaffolding of de novo genome assemblies based on chromatin interactions. *Nat Biotechnol*, 31(12):1119-1125. https://doi.org/10.1038/nbt.2727

Cao D, Gao X, Liu J, et al., 2012. Root-specific DNA methylation in chloris virgata, a natural alkaline-resistant halophyte, in response to salt and alkaline stresses. *Plant Molecular Biology Reporter*, 30(5):1102-1109. https://doi.org/10.1007/s11105-012-0420-z

Cao S, Chen K, Lu K, et al., 2023. Asymmetric variation in DNA methylation during domestication and de-domestication of rice. *Plant Cell*, 35(9):3429-3443. https://doi.org/10.1093/plcell/koad160

Chan SW, Henderson IR, Jacobsen SE, 2005. Gardening the genome: DNA methylation in arabidopsis thaliana. *Nat Rev Genet*, 6(5):351-360. https://doi.org/10.1038/nrg1601

Chang JS, Lin ZX, Liu YJ, et al., 2021. Ultra performance liquid chromatography-tandem mass spectrometry assay for the quantification of rna and DNA methylation. *J Pharm Biomed Anal*, 197:113969. https://doi.org/10.1016/j.jpba.2021.113969

Chen C, Wang M, Zhu J, et al., 2022a. Long-term effect of epigenetic modification in plant-microbe interactions: Modification of DNA methylation induced by plant growth-promoting bacteria mediates promotion process. *Microbiome*, 10(1):36. https://doi.org/10.1186/s40168-022-01236-9

Chen J, Liu J, Jiang J, et al., 2021. F-box protein cfk1 interacts with and degrades de novo DNA methyltransferase in arabidopsis. *New Phytol*, 229(6):3303-3317. https://doi.org/10.1111/nph.17103

Chen K, Shi Z, Zhang S, et al., 2022b. Methylation and expression of rice nlr genes after low temperature stress. *Gene*, 845:146830. https://doi.org/10.1016/j.gene.2022.146830

Chen R, Li M, Zhang H, et al., 2019. Continuous salt stress-induced long non-coding rnas and DNA methylation patterns in soybean roots. *BMC Genomics*, 20(1):730. https://doi.org/10.1186/s12864-019-6101-7

Chu Q, Gong X, Hu Y, et al., 2025. The DNA methylomes of echinochloa species provide insights into polyploidization-driven adaptation and orphan crop domestication. *Plant J*, 121(3):e70033. https://doi.org/10.1111/tpj.70033

Dai X, Wang J, Song Y, et al., 2021. Cytosine methylation of the fwa promoter promotes direct in vitro shoot regeneration in arabidopsis thaliana. *J Integr Plant Biol*, 63(8):1491-1504. https://doi.org/10.1111/jipb.13156

Deleris A, Halter T, Navarro L, 2016. DNA methylation and demethylation in plant immunity. *Annu Rev Phytopathol*, 54:579-603. https://doi.org/10.1146/annurev-phyto-080615-100308

Ding H, Gao J, Qin C, et al., 2014. The dynamics of DNA methylation in maize roots under pb stress. *Int J Mol Sci*, 15(12):23537-23554. https://doi.org/10.3390/ijms151223537

Unedited

Duan CG, Zhu JK, Cao X, 2018. Retrospective and perspective of plant epigenetics in china. *J Genet Genomics*, 45(11):621-638. https://doi.org/10.1016/j.jgg.2018.09.004
Feil R, Berger F, 2007. Convergent evolution of genomic imprinting in plants and mammals. *Trends Genet*, 23(4):192-199. https://doi.org/10.1016/j.tig.2007.02.004
Feng S, Cokus SJ, Zhang X, et al., 2010. Conservation and divergence of methylation patterning in plants and animals. *Proc Natl Acad Sci U S A*, 107(19):8689-8694. https://doi.org/10.1073/pnas.1002720107
Filek M, Keskinen R, Hartikainen H, et al., 2008. The protective role of selenium in rape seedlings subjected to cadmium stress. *J Plant Physiol*, 165(8):833-844. https://doi.org/10.1016/j.jplph.2007.06.006
Francischini J, Kemper EL, Costa JB, et al., 2017. DNA methylation in sugarcane somaclonal variants assessed through methylation-sensitive amplified polymorphism. *Genet Mol Res*, 16(2) https://doi.org/10.4238/gmr16029585
Giannelli G, Fasani E, Dalcorso G, 2024. Epigenetics of heavy metal stress and response in plants. *Front Biosci (Schol Ed)*, 16(2):13. https://doi.org/10.31083/j.fbs1602013
Gong Z, Morales-Ruiz T, Ariza RR, et al., 2002. Ros1, a repressor of transcriptional gene silencing in arabidopsis, encodes a DNA glycosylase/lyase. *Cell*, 111(6):803-814. https://doi.org/10.1016/s0092-8674(02)01133-9
Gu C, Pei MS, Guo ZH, et al., 2024. Multi-omics provide insights into the regulation of DNA methylation in pear fruit metabolism. *Genome Biol*, 25(1):70. https://doi.org/10.1186/s13059-024-03200-2
Gu H, Smith ZD, Bock C, et al., 2011. Preparation of reduced representation bisulfite sequencing libraries for genome-scale DNA methylation profiling. *Nat Protoc*, 6(4):468-481. https://doi.org/10.1038/nprot.2010.190
Guarino F, Cicatelli A, Brundu G, et al., 2015. Epigenetic diversity of clonal white poplar (populus alba l.) populations: Could methylation support the success of vegetative reproduction strategy? *PLoS One*, 10(7):e0131480. https://doi.org/10.1371/journal.pone.0131480
Halter T, Wang J, Amesefe D, et al., 2021. The arabidopsis active demethylase ros1 cis-regulates defence genes by erasing DNA methylation at promoter-regulatory regions. *Elife*, 10 https://doi.org/10.7554/eLife.62994
He L, Huang H, Bradai M, et al., 2022. DNA methylation-free arabidopsis reveals crucial roles of DNA methylation in regulating gene expression and development. *Nat Commun*, 13(1):1335. https://doi.org/10.1038/s41467-022-28940-2
Hou Z, Dai J, Wang C, et al., 2022. Rll5, an f-box-containing protein, involved in preventing transgene silencing and in maintaining global DNA methylation in arabidopsis. *Biochem Biophys Res Commun*, 609:1-8. https://doi.org/10.1016/j.bbrc.2022.03.135
Ibarra CA, Feng X, Schoft VK, et al., 2012. Active DNA demethylation in plant companion cells reinforces transposon methylation in gametes. *Science*, 337(6100):1360-1364. https://doi.org/10.1126/science.1224839
Jagić M, Vuk T, Škiljaica A, et al., 2022. Bpm1 regulates rddm-mediated DNA methylation via a cullin 3 independent mechanism. *Plant Cell Rep*, 41(11):2139-2157. https://doi.org/10.1007/s00299-022-02911-9
Kawakatsu T, Nery JR, Castanon R, et al., 2017. Dynamic DNA methylation reconfiguration during seed development and germination. *Genome Biol*, 18(1):171. https://doi.org/10.1186/s13059-017-1251-x
Kenchanmane Raju SK, Ledford M, Niederhuth CE, 2023. DNA methylation signatures of duplicate gene evolution in angiosperms. *Plant Physiol*, 192(4):2883-2901. https://doi.org/10.1093/plphys/kiad220
Kong L, Liu Y, Wang X, et al., 2020. Insight into the role of epigenetic processes in abiotic and biotic stress response in wheat and barley. *Int J Mol Sci*, 21(4) https://doi.org/10.3390/ijms21041480
Kumar G, Rattan UK, Singh AK, 2016. Chilling-mediated DNA methylation changes during dormancy and its release reveal the importance of epigenetic regulation during winter dormancy in apple (malus x domestica borkh.). *PLoS One*, 11(2):e0149934. https://doi.org/10.1371/journal.pone.0149934
Law JA, Jacobsen SE, 2010. Establishing, maintaining and modifying DNA methylation patterns in plants and animals. *Nat Rev Genet*, 11(3):204-220. https://doi.org/10.1038/nrg2719
Lei M, La H, Lu K, et al., 2014. Arabidopsis edm2 promotes ibm1 distal polyadenylation and regulates genome DNA methylation patterns. *Proc Natl Acad Sci U S A*, 111(1):527-532. https://doi.org/10.1073/pnas.1320106110
Leutwiler LS, Hough-Evans BR, Meyerowitz EM, 1984. The DNA of arabidopsis thaliana. *Molecular and General Genetics MGG*, 194(1):15-23. https://doi.org/10.1007/BF00383491
Li D, Zhang B, Xing X, et al., 2015. Combining medip-seq and mre-seq to investigate genome-wide cpg methylation. *Methods*, 72:29-40. https://doi.org/10.1016/j.ymeth.2014.10.032
Li D, Du J, Gao M, et al., 2024. Identification of atalkbh1a and atalkbh1d as DNA n(6)-adenine demethylases in arabidopsis thaliana. *Plant Sci*, 342:112055. https://doi.org/10.1016/j.plantsci.2024.112055
Li Y, Guo D, 2023. Transcriptome and DNA methylome analysis of two contrasting rice genotypes under salt stress during germination. *Int J Mol Sci*, 24(4) https://doi.org/10.3390/ijms24043978
Li Z, Liu Q, Zhao K, et al., 2023. Dynamic DNA methylation modification in peanut seed development. *iScience*, 26(7):107062. https://doi.org/10.1016/j.isci.2023.107062
Liang D, Zhang Z, Wu H, et al., 2014. Single-base-resolution methylomes of populus trichocarpa reveal the association between DNA methylation and drought stress. *BMC Genet*, 15 Suppl 1(Suppl 1):S9. https://doi.org/10.1186/1471-2156-15-s1-s9
Lieberman-Aiden E, Van Berkum NL, Williams L, et al., 2009. Comprehensive mapping of long-range interactions reveals folding principles of the human genome. *Science*, 326(5950):289-293. https://doi.org/10.1126/science.1181369
Lindroth AM, Saarikoski P, Flygh G, et al., 2001. Two s-adenosylmethionine synthetase-encoding genes differentially expressed during adventitious root development in pinus contorta. *Plant Mol Biol*, 46(3):335-346. https://doi.org/10.1023/a:1010637012528

Unedited

Lisanti S, Omar WA, Tomaszewski B, et al., 2013. Comparison of methods for quantification of global DNA methylation in human cells and tissues. *PLoS One*, 8(11):e79044. https://doi.org/10.1371/journal.pone.0079044
Lister R, Pelizzola M, Dowen RH, et al., 2009. Human DNA methylomes at base resolution show widespread epigenomic differences. *Nature*, 462(7271):315-322. https://doi.org/10.1038/nature08514
Luo C, Hajkova P, Ecker JR, 2018. Dynamic DNA methylation: In the right place at the right time. *Science*, 361(6409):1336-1340. https://doi.org/10.1126/science.aat6806
Meissner A, Gnirke A, Bell GW, et al., 2005. Reduced representation bisulfite sequencing for comparative high-resolution DNA methylation analysis. *Nucleic Acids Res*, 33(18):5868-5877. https://doi.org/10.1093/nar/gki901
Miao W, Dai J, Wang Y, et al., 2021. Roles of idm3 and sdj1/2/3 in establishment and/or maintenance of DNA methylation in arabidopsis. *Plant Cell Physiol*, 62(9):1409-1422. https://doi.org/10.1093/pcp/pcab091
Moore LD, Le T, Fan G, 2013. DNA methylation and its basic function. *Neuropsychopharmacology*, 38(1):23-38. https://doi.org/10.1038/npp.2012.112
Nakabayashi K, Yamamura M, Haseagawa K, et al., 2023. Reduced representation bisulfite sequencing (rrbs). *Methods Mol Biol*, 2577:39-51. https://doi.org/10.1007/978-1-0716-2724-2_3
Niederhuth CE, Bewick AJ, Ji L, et al., 2016. Widespread natural variation of DNA methylation within angiosperms. *Genome Biol*, 17(1):194. https://doi.org/10.1186/s13059-016-1059-0
Ning YQ, Liu N, Lan KK, et al., 2020. Dream complex suppresses DNA methylation maintenance genes and precludes DNA hypermethylation. *Nat Plants*, 6(8):942-956. https://doi.org/10.1038/s41477-020-0710-7
Olova N, Krueger F, Andrews S, et al., 2018. Comparison of whole-genome bisulfite sequencing library preparation strategies identifies sources of biases affecting DNA methylation data. *Genome Biol*, 19(1):33. https://doi.org/10.1186/s13059-018-1408-2
Ouyang W, Xiong D, Li G, et al., 2020. Unraveling the 3d genome architecture in plants: Present and future. *Mol Plant*, 13(12):1676-1693. https://doi.org/10.1016/j.molp.2020.10.002
Quadrana L, Colot V, 2016. Plant transgenerational epigenetics. *Annu Rev Genet*, 50:467-491. https://doi.org/10.1146/annurev-genet-120215-035254
Rimoldi M, Wang N, Zhang J, et al., 2024. DNA methylation patterns of transcription factor binding regions characterize their functional and evolutionary contexts. *Genome Biol*, 25(1):146. https://doi.org/10.1186/s13059-024-03218-6
Rosellini D, Ferradini N, Allegrucci S, et al., 2016. Sexual polyploidization in medicago sativa l.: Impact on the phenotype, gene transcription, and genome methylation. *G3 (Bethesda)*, 6(4):925-938. https://doi.org/10.1534/g3.115.026021
Ruden DM, Garfinkel MD, Sollars VE, et al., 2003. Waddington's widget: Hsp90 and the inheritance of acquired characters. *Semin Cell Dev Biol*, 14(5):301-310. https://doi.org/10.1016/j.semcdb.2003.09.024
Saini A, Rawat Y, Jain K, et al., 2023. State-of-the-art techniques to study epigenetics. *Prog Mol Biol Transl Sci*, 197:23-50. https://doi.org/10.1016/bs.pmbts.2023.02.004
Sala-Cholewa K, Tomasiak A, Nowak K, et al., 2024. DNA methylation analysis of floral parts revealed dynamic changes during the development of homostylous fagopyrum tataricum and heterostylous f. Esculentum flowers. *BMC Plant Biol*, 24(1):448. https://doi.org/10.1186/s12870-024-05162-w
Song Q, Zhang T, Stelly DM, et al., 2017. Epigenomic and functional analyses reveal roles of epialleles in the loss of photoperiod sensitivity during domestication of allotetraploid cottons. *Genome Biol*, 18(1):99. https://doi.org/10.1186/s13059-017-1229-8
Srikant T, Yuan W, Berendzen KW, et al., 2022. Canalization of genome-wide transcriptional activity in arabidopsis thaliana accessions by met1-dependent cg methylation. *Genome Biol*, 23(1):263. https://doi.org/10.1186/s13059-022-02833-5
Stroud H, Do T, Du J, et al., 2014. Non-cg methylation patterns shape the epigenetic landscape in arabidopsis. *Nat Struct Mol Biol*, 21(1):64-72. https://doi.org/10.1038/nsmb.2735
Takuno S, Ran JH, Gaut BS, 2016. Evolutionary patterns of genic DNA methylation vary across land plants. *Nat Plants*, 2:15222. https://doi.org/10.1038/nplants.2015.222
Tan F, Zhou C, Zhou Q, et al., 2016. Analysis of chromatin regulators reveals specific features of rice DNA methylation pathways. *Plant Physiol*, 171(3):2041-2054. https://doi.org/10.1104/pp.16.00393
Tian W, Zhou J, Bartlett A, et al., 2023. Single-cell DNA methylation and 3d genome architecture in the human brain. *Science*, 382(6667):eadf5357. https://doi.org/10.1126/science.adf5357
Walkowiak S, Gao L, Monat C, et al., 2020. Multiple wheat genomes reveal global variation in modern breeding. *Nature*, 588(7837):277-283. https://doi.org/10.1038/s41586-020-2961-x
Wambui Mbichi R, Wang QF, Wan T, 2020. Rna directed DNA methylation and seed plant genome evolution. *Plant Cell Rep*, 39(8):983-996. https://doi.org/10.1007/s00299-020-02558-4
Wang H, Lu H, Yang Z, et al., 2023a. Characterization of lodging variation of weedy rice. *J Exp Bot*, 74(5):1403-1419. https://doi.org/10.1093/jxb/erac480
Wang L, Zheng K, Zeng L, et al., 2022a. Reinforcement of chh methylation through rna-directed DNA methylation ensures sexual reproduction in rice. *Plant Physiol*, 188(2):1189-1209. https://doi.org/10.1093/plphys/kiab531
Wang L, Zhang J, Xu X, 2024. A comparison of DNA-methylation during protoplast culture of ponkan mandarin (citrus reticulata blanco) and tobacco (nicotiana tabacum l.). *Plants (Basel)*, 13(20) https://doi.org/10.3390/plants13202878
Wang Q, La Y, Xia H, et al., 2022b. Roles of mem1 in safeguarding arabidopsis genome against DNA damage, inhibiting atm/sog1-mediated DNA damage response, and antagonizing global DNA hypermethylation. *J Integr Plant Biol*, 64(1):87-104. https://doi.org/10.1111/jipb.13200

Unedited

Wang Y, Zhang H, Gu J, et al., 2023b. The sink-source relationship in cucumber (cucumis sativus l.) is modulated by DNA methylation. *Plants (Basel)*, 13(1) https://doi.org/10.3390/plants13010103
Weber M, Davies JJ, Wittig D, et al., 2005. Chromosome-wide and promoter-specific analyses identify sites of differential DNA methylation in normal and transformed human cells. *Nat Genet*, 37(8):853-862. https://doi.org/10.1038/ng1598
Wibowo A, Becker C, Marconi G, et al., 2016. Hyperosmotic stress memory in arabidopsis is mediated by distinct epigenetically labile sites in the genome and is restricted in the male germline by DNA glycosylase activity. *Elife*, 5 https://doi.org/10.7554/eLife.13546
Xie H, Sun Y, Cheng B, et al., 2019. Variation in ice1 methylation primarily determines phenotypic variation in freezing tolerance in arabidopsis thaliana. *Plant Cell Physiol*, 60(1):152-165. https://doi.org/10.1093/pcp/pcy197
Xie H, Li X, Sun Y, et al., 2024. DNA methylation of the autonomous pathway is associated with flowering time variations in arabidopsis thaliana. *Int J Mol Sci*, 25(13) https://doi.org/10.3390/ijms25137478
Xing MQ, Zhang YJ, Zhou SR, et al., 2015. Global analysis reveals the crucial roles of DNA methylation during rice seed development. *Plant Physiol*, 168(4):1417-1432. https://doi.org/10.1104/pp.15.00414
Xu JH, Irshad F, Yan Y, et al., 2022. Loss of function of the rrmf domain in osros1a causes sterility in rice (oryza sativa l.). *Int J Mol Sci*, 23(19) https://doi.org/10.3390/ijms231911349
Xu L, Yuan K, Yuan M, et al., 2020. Regulation of rice tillering by rna-directed DNA methylation at miniature inverted-repeat transposable elements. *Mol Plant*, 13(6):851-863. https://doi.org/10.1016/j.molp.2020.02.009
Xu YC, Zhang J, Zhang DY, et al., 2021. Identification of long noncoding natural antisense transcripts (lncnats) correlated with drought stress response in wild rice (oryza nivara). *BMC Genomics*, 22(1):424. https://doi.org/10.1186/s12864-021-07754-4
Yang JL, Liu LW, Gong YQ, et al., 2007. [analysis of genomic DNA methylation level in radish under cadmium stress by methylation-sensitive amplified polymorphism technique]. *Zhi Wu Sheng Li Yu Fen Zi Sheng Wu Xue Xue Bao*, 33(3):219-226.
Yang L, Lang C, Wu Y, et al., 2022. Ros1-mediated decrease in DNA methylation and increase in expression of defense genes and stress response genes in arabidopsis thaliana due to abiotic stresses. *BMC Plant Biol*, 22(1):104. https://doi.org/10.1186/s12870-022-03473-4
Yao WJ, Wang YP, Peng J, et al., 2024. The rpt2a-met1 axis regulates terminal flower1 to control inflorescence meristem indeterminacy in arabidopsis. *Plant Cell*, 36(5):1718-1735. https://doi.org/10.1093/plcell/koad249
Yu Y, Wang S, Wang Z, et al., 2023. Arabidopsis thaliana: A powerful model organism to explore histone modifications and their upstream regulations. *Epigenetics*, 18(1):2211362. https://doi.org/10.1080/15592294.2023.2211362
Yuan J, Jiao W, Liu Y, et al., 2020. Dynamic and reversible DNA methylation changes induced by genome separation and merger of polyploid wheat. *BMC Biol*, 18(1):171. https://doi.org/10.1186/s12915-020-00909-x
Yuan JL, Sun HM, Guo GP, et al., 2014. Correlation between DNA methylation and chronological age of moso bamboo (phyllostachys heterocycla var. Pubescens). *Bot Stud*, 55(1):4. https://doi.org/10.1186/1999-3110-55-4
Yung WS, Wang Q, Chan LY, et al., 2024. DNA hypomethylation is one of the epigenetic mechanisms involved in salt-stress priming in soybean seedlings. *Plant Cell Environ*, https://doi.org/10.1111/pce.15297
Zhang H, Ali A, Hou F, et al., 2018a. Effects of ploidy variation on promoter DNA methylation and gene expression in rice (oryza sativa l.). *BMC Plant Biol*, 18(1):314. https://doi.org/10.1186/s12870-018-1553-5
Zhang H, Lang Z, Zhu JK, 2018b. Dynamics and function of DNA methylation in plants. *Nat Rev Mol Cell Biol*, 19(8):489-506. https://doi.org/10.1038/s41580-018-0016-z
Zhang L, Yu H, Ma B, et al., 2017. A natural tandem array alleviates epigenetic repression of ipa1 and leads to superior yielding rice. *Nat Commun*, 8:14789. https://doi.org/10.1038/ncomms14789
Zhang X, Yazaki J, Sundaresan A, et al., 2006. Genome-wide high-resolution mapping and functional analysis of DNA methylation in arabidopsis. *Cell*, 126(6):1189-1201. https://doi.org/10.1016/j.cell.2006.08.003
Zhao L, Wang P, Hou H, et al., 2014. Transcriptional regulation of cell cycle genes in response to abiotic stresses correlates with dynamic changes in histone modifications in maize. *PLoS One*, 9(8):e106070. https://doi.org/10.1371/journal.pone.0106070
Zheng S, Chen J, He Y, et al., 2024. The osago2-osnac300-osnap module regulates leaf senescence in rice. *J Integr Plant Biol*, 66(11):2395-2411. https://doi.org/10.1111/jipb.13766
Zhong X, 2016. Comparative epigenomics: A powerful tool to understand the evolution of DNA methylation. *New Phytol*, 210(1):76-80. https://doi.org/10.1111/nph.13540
Zhou C, Wei X, Liu S, et al., 2024. Global characterization of DNA methylation during rice leaf angle development. *J Agric Food Chem*, 72(34):19219-19231. https://doi.org/10.1021/acs.jafc.4c02650
Zhou L, Tian S, Qin G, 2019. Rna methylomes reveal the m(6)a-mediated regulation of DNA demethylase gene sldml2 in tomato fruit ripening. *Genome Biol*, 20(1):156. https://doi.org/10.1186/s13059-019-1771-7
Zhou X, Wei M, Nie W, et al., 2022. The h3k9me2-binding protein agdp3 limits DNA methylation and transcriptional gene silencing in arabidopsis. *J Integr Plant Biol*, 64(12):2385-2395. https://doi.org/10.1111/jipb.13369
Zhu H, Liu T, Wang Z, 2023a. Schime: Predicting single-cell DNA methylation levels based on single-cell hi-c data. *Brief Bioinform*, 24(4) https://doi.org/10.1093/bib/bbad223
Zhu W, Huang J, Huang M, et al., 2023b. Atac-me simultaneously decodes chromatin accessibility and DNA methylation. *Trends Plant Sci*, 28(8):968-969. https://doi.org/10.1016/j.tplants.2023.05.013
Zicola J, Liu L, Tänzler P, et al., 2019. Targeted DNA methylation represses two enhancers of flowering locus t in arabidopsis

Unedited

thaliana. *Nat Plants*, 5(3):300-307. https://doi.org/10.1038/s41477-019-0375-2

Supplementary information
Tables S1 and S2; Figs. S1 and S2

Unedited