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The m^{6}A writers, readers, and erasers regulate plant development and respond to biotic/abiotic stresses

Yingqi Shi[1#], Songlin Yang[1#], Tiantian Pei[1], Yifan Xu[1], Yibing Zhao[1], Hao Xue[1], Xinyue Ma[1], Huazhong Ren[1,2,3*] and Xingwang Liu[1,2,3*]

[1] *Department of Vegetable Science, College of Horticulture, China Agricultural University, Beijing 100193, China*
[2] *Sanya Institute of China Agricultural University, Sanya 572019, China*
[3] *Frontier Technology Research Institute of China Agricultural University, Shenzhen 518000, China*
[#] Authors contributed equally: Yingqi Shi, Songlin Yang
* Corresponding authors, E-mail: renhuazhong@cau.edu.cn; liuxw01@cau.edu.cn

Abstract

N6-methyladenosine (m^{6}A) is the predominant internal mRNA modification with dynamic and reversible regulation on almost all aspects of mRNA metabolism, including mRNA stability, splicing, and translation. Three m^{6}A-related proteins 'writers, readers, and erasers' collaborate to regulate the entire process of m^{6}A modification within the organism. The MeRIP-seq technology has expedited research on m^{6}A modifications in plants. Although the distribution of m^{6}A sites varies across plant species, they are predominantly enriched near the stop codon and within the 3' untranslated region (3'UTR) of mRNAs. Beyond its essential roles in plant growth and development, m^{6}A also critically regulates plant responses to biotic and abiotic stresses. This review not only systematically reviews the writers, readers, and erasers associated with m^{6}A modification, but also comprehensively summarizes recent advancements in elucidating the significance of m^{6}A in plant organ development, floral transition, and fruit ripening. Furthermore, we discuss how m^{6}A influences plant-virus relationships and environmental signals. In summary, analyzing m^{6}A modification is expected to show promise in creating crop varieties with enhanced yield, quality, and stress tolerance.

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Introduction

Regulating gene expression by chemical modifications is epigenetic regulation, mainly involving DNA/RNA/histone modifications[1]. With the high sensitivity of modern molecular biology techniques and detection methods, RNA modification has entered a golden era[2]. Various post-transcriptional modifications of RNA provide a chemical basis for its functional diversification. Among the more than 170 RNA modifications that have been identified so far, N6-methyladenosine (m^{6}A) has been intensively investigated due to its unique functions[3]. m^{6}A occurs when a methyl group is added to the N atom at position 6 of adenine in mRNA molecules. It is found in mRNA, tRNA, rRNA, snRNA, and ncRNA across a wide range of eukaryotic species, spanning from yeast (*Saccharomyces*) to humans (*Homo sapiens*)[4]. In plants, the m^{6}A modification of mRNA accounts for about 0.45% to 0.65% of all adenosines, which is higher than the 0.1% to 0.4% found in mammals[5]. As sequencing technology improves by leaps and bounds, m^{6}A methylation maps of many plants like *Arabidopsis* (*Arabidopsis thaliana*), rice (*Oryza sativa* L.)[6], cotton (*Gossypium hirsutum* L.)[7], soybean (*Glycine max*)[8] , and Pak-choi (*Brassica rapa* ssp. *Chinensis*)[9] have been mapped successfully. Although the distribution of m^{6}A modification may differ among species, tissues, and diverse environmental conditions, the distribution of m^{6}A modifications near mRNA stop codons and within 3'UTRs represents an evolutionarily conserved feature across species[10]. Moreover, m^{6}A modifications in the 5'UTR predominantly influence mRNA translation, while those in the 3'UTR primarily regulate mRNA stability. For instance, in wheat (*Triticum aestivum* L.), the m^{6}A modifications within the start codon, and the 5'UTR are capable of enhancing mRNA translation[11]. In apples (*Malus domestica* Borkh.), *MdMTA* positively regulates the 5'UTR m^{6}A modification of *Md4CL3* to improve drought tolerance[12]. The m^{6}A modification is predominantly added in mammals and plants within the 'RRACH' (R = A/G, H = A/C/U), while the 'URUAY' (R = A/G, Y = U/C) motif is identified as a conserved m^{6}A plant-exclusive pattern[13]. Notably, a MeRIP-seq analysis of wheat revealed a notable enrichment of 'GAACU' in the m^{6}A peaks[14]. The value of m^{6}A modification in plants has been extensively researched, particularly in model plant species. Evidence indicates that m^{6}A methylation is actively involved in diverse plant physiological processes, including plant embryogenesis[15], leaf and root development, trichome branching[16], flowering transition[17], fruit ripening[18], viral infection[19], and abiotic stress response. While RNA methylation is crucial in plants, our comprehension of m^{6}A is in its early stages. This review concisely summarises the current research regarding m^{6}A methylation in plants, emphasizing the importance of elucidating mRNA post-transcriptional modification mechanisms, and leveraging m^{6}A-associated genes for enhancing crop breeding practices.

Major components of m^{6}A modification

The m^{6}A modification is dynamically and reversibly regulated by three functional protein groups: methyltransferases (writers) catalyze this modification, m^{6}A-binding proteins (readers) recognize it, and demethylases (erasers) remove it[20]. These three protein groups collaborate to regulate the entire m^{6}A modification process within organisms (Fig. 1). Furthermore, the abundance of these three m^{6}A-related proteins varies significantly across different tissues and species. For example, in pigeon pea (*Cajanus cajan* [L.] Millspaugh), quantitative analysis of m^{6}A regulator expression (*CcMTA/B, CcFIPA/B, CcALKBH1/2/8/9/10*) across developmental stages revealed tissue-specific patterns, with maximal transcript

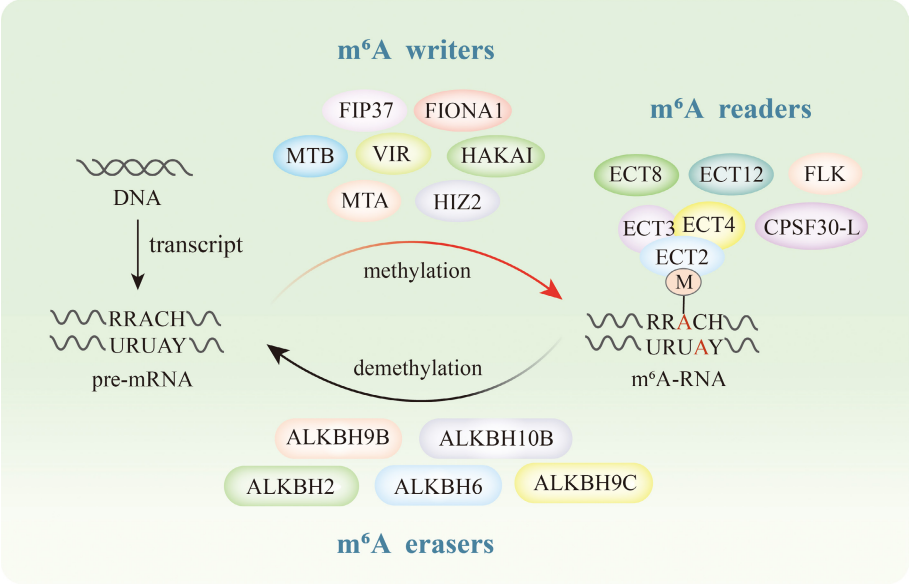

Fig. 1 m^{6}A modification related proteins in plants. The writers involved in m^{6}A modification include MTA, MTB, VIR, FIP37, HAKAI, FIONA1, and HIZ2. The readers include ECT2, ECT3, ECT4, ECT8, ECT12, CPSF30-L, and FLK. The erasers include ALKBH2, ALKBH6, ALKBH9B, ALKBH9C, and ALKBH10B.

levels in leaves and minimal accumulation in roots[21]. Moreover, tissue-specific expression patterns were observed for tomato *ALKBH homologs*, with *SlALKBH9A* showing ripening-stage-dependent regulation, and further RT-qPCR analysis indicated high expression of *SlYTH1* in young tissue (YL) , and of *SlYTH3A* in aging tissues (ML and SL)[22].

Writers

m^{6}A methyltransferase (writer) is a class of protein that can add methyl modifications to the N6 position on the adenine of mRNA. S-adenosylmethionine (SAM) is commonly utilized as a methyl contributor in methylation procedures. m^{6}A writer members function primarily in a complex form, the earliest known methyltransferase in mammals was the METTL3 protein, which can form a methyltransferase complex with METTL14, HAKAI, and WTAP to transfer methyl groups[23]. At present, members of the m^{6}A methyltransferase have been identified in plants, including MTA (methyltransferase A), MTB (methyltransferase B), FIP37 (FKBP12 INTERACTING PROTEIN 37 KD), VIR (VIRILIZER), FIO1 (FIONA1), HAKAI (HAKAI ubiquitin E3 ligase)[24], and HIZ2[25]. Similar to mammals, in plants, MTA, MTB, FIP37, and HAKAI can also form homologous or heterogeneous aggregates to transfer methyl groups, and the m^{6}A writers in plants recognize the conservative motifs 'RRACH' or 'URUAY'. In *Arabidopsis*, MTA exhibits high expression levels within the reproductive organs, meristem tissues, and new lateral roots, however, *mta* mutations cause plant embryos to fail to develop normally. In addition, it was found that MTA can promote the formation of mature miRNA393b through methylation of pre-miRNA393b and enhance the response of *Arabidopsis* to auxin[26]. In mammals, WTAP could facilitate the recruitment of METTL3 and METTL14 to influence mRNA splicing[27]. However, WTAP homologous protein in plant FIP37 is dispersed throughout the nucleoplasm and has no observed impact on RNA splicing. FIP37-deficient plants exhibit excessive cellular proliferation within shoot apical meristems, and their self-pollinated seeds show premature bleaching, indicating that m^{6}A writers could control meristematic cell division[28]. The U6 snRNA is an essential component of the spliceosome, and FIONA1 is an *Arabidopsis* U6 m^{6}A methyltransferase that installs m^{6}A in U6 snRNA and a small subset of poly(A)+ RNA, several studies have demonstrated that FIONA1 affects plant flowering[29]. HAKAI is a considerable factor in impacting the formation of the root vascular system in *Arabidopsis* and specifically interacts with the zinc finger protein HIZ2 to accelerate the binding to MTA. Notably, HIZ2 remains associated with MTA even in the absence of HAKAI, this suggests that HIZ2 might be the plant homolog of ZC3H13 (the zinc finger CCCH domain-containing protein 13, which functions as m^{6}A-METTL associated complex in animals)[25]. Additionally, except for HAKAI, the absence of m^{6}A methyltransferase FIP37, VIR, MTA, and MTB can lead to abnormal development of plant embryos, such as loss of MdMTA in apple and OsMTA in rice[30]. Hence, the study of m^{6}A writers mainly uses weak allelic mutation, partial complement, or knockdown to study the role of m^{6}A writers while circumventing lethal phenotypes in numerous studies. Further research is required to validate the roles of these potential methyltransferases and to assess their functional conservation and species-specific characteristics.

Readers

m^{6}A readers, also known as m^{6}A binding proteins, do not directly affect the overall m^{6}A level by themselves but play a regulatory role by binding m^{6}A-RNA. m^{6}A readers possess the YT521 - B (YTH) domain, which constructs a hydrophobic pocket enabling it to bind the m^{6}A constituents. In mammals, five YTH proteins have been recognized, such as YTHDF1/2/3 and YTHDC1/2[31]. There are 13 YTH homologous proteins in plants, and 11 of them have evolutionarily highly conserved C-terminus, further divided into three branches of ABC, YTHDF-A (ECT1/2/3/4), YTHDF-B (ECT5/9/10), YTHDF-C (ECT6/7/8/11)[32]. Recently, ECT12 was identified as a novel m^{6}A reader that contains the N-terminal YTH domain[33]. Currently, only ECT2/3/4/8/12 and CPSF30-L which localizes to the nucleus have been identified as m^{6}A reading proteins. Analysis of ECT2 reveals that it exists in both the nucleus and the cytoplasm, functioning respectively in 3'UTR processing and promoting mRNA stability. CPSF30-L modulates the alternative polyadenylation (APA) of pre-mRNA for the regulation of poly(A) site selection[34]. Recent studies have shown that m^{6}A readers affect many key biological processes during the ontogenesis of plants. For instance, in *Arabidopsis*, a mutant of *ect2* speeds up the degradation of three trichome morphogenesis transcripts[16]. Several researches have shown that ECT2/3/4 function collaboratively to promote cellular proliferation

in organ primordia. The phenotype of double mutant *ect2/3* is retarded growth on root, leaf, stem, and flower, and ECT2/3/4 redundantly impacts seed germination by regulating ABA access[35,36]. Wu et al. discovered that ECT2 boosts the expression of various 20S subunits, leading to increased proteasome function, marking the initial proof of epitranscriptomic control over the 20S proteasome[37]. Furthermore, ECT1/2 interacts specifically with the stress response protein CIPK1, aiding in transmitting calcium signaling to the plant nucleus in reaction to various external stimuli. Recently, evidence has emerged showing that ECT8-mediated stabilization and destabilization of the genes encoding salt stress positive or negative regulators, respectively, contribute to the salt stress tolerance of *Arabidopsis*[38]. ECT12 is identified as a novel m^{6}A reader, which impacts the steadiness of mRNAs associated with drought and salt stress responses[33]. Beyond the YTH-domain proteins, those harboring the KH-domain proteins are also considered as prospective m^{6}A readers. FLK (flowering-associated protein K), which is homologous to IGF2BP (an m^{6}A reader in humans with four KH domains), has been recognized as an m^{6}A reader and exerts an impact on the floral transition in *Arabidopsis*[39].

Erasers

m^{6}A erasers are of vital importance in converting methylated nucleotides back to their unmodified form. Following the discovery of m^{6}A, it was initially regarded as a stable and unchanging methylation mark. However, in 2011, *in vitro* experiments successfully demonstrated the demethylation of m^{6}A-modified mRNA using FTO proteins, marking the first identification of a demethylase capable of removing m^{6}A modifications, thus revealing that m^{6}A is reversible[40]. In plants, no FTO homologs have been identified, however, six ALKBH proteins exhibiting demethylase activity have been discovered. These include AtALKBH6, AtALKBH9B, AtALKBH10B, and AtALKBH9C in *Arabidopsis*[41,42], SLALKBH2 in tomato (*Solanum lycopersicum*)[43], and GhALKBH10B in *Gossypium hirsutum*[44]. AtALKBH10B is in the nucleus of the cell, the *alkbh10b* mutant showed a delayed flowering phenotype. MeRIP high-throughput sequencing of alkbh10b showed that about 1190 mRNAs had an up-regulated m^{6}A level in *Arabidopsis*, indicating that ALKBH protein impacts the process of plant flowering transformation by regulating downstream gene m^{6}A level[17]. Another eraser protein AtALKBH9B mediates mRNA silencing and degradation pathways by recruiting siRNA to P-bodies, and it interacts with the AMV, thereby increasing the virus's capacity to infect host cells[45]. Recent research indicates that m^{6}A methylation can significantly influence crop productivity, specifically, m^{6}A demethylation can boost the biomass and yields of rice and potato by 50%[46]. Interestingly, although these erasers have the function of removing m^{6}A from RNA, the targets of different erasers may vary, and the mechanism of action of selective removal of m^{6}A from different target genes among erasers is not clear.

m^{6}A regulates mRNA metabolism

m^{6}A is a highly conserved post-transcriptional modification process that governs the genetic information of eukaryotic organisms. This modification exerts various effects on mRNA functionality, such as influencing stability, splicing, translation, and miRNA processing (Fig. 2).

Stability of mRNA

The genetic central dogma tells us that mRNA serves as the foundation for protein translation and is pivotal in gene expression. Recent studies have employed mutants of m^{6}A writers, readers, and erasers to systematically elucidate the influence of m^{6}A modification on mRNA stability, which subsequently modulates the expression of key genes regulating plant development. Several studies have demonstrated that m^{6}A modification is generally negatively correlated with mRNA stability. For example, in the *alkbh10b* mutant of *Arabidopsis*, the m^{6}A modification level of *Flowering locus T* (*FT*) mRNA increased, resulting in the mRNA stability and gene expression level decreased[17]. In tomato, m^{6}A demethylase SlALKBH2 decreased mRNA degradation rate and promoted mRNA stability[43]. Moreover, the reduction of m^{6}A on SPL3 and SEP3 transcripts leads to increased stability in *fio1* mutants. However, studies have shown that low expression of *MTA* triggered a drop in mRNA stability and gene expression abundance in *Arabidopsis* and strawberry of *NCED5*

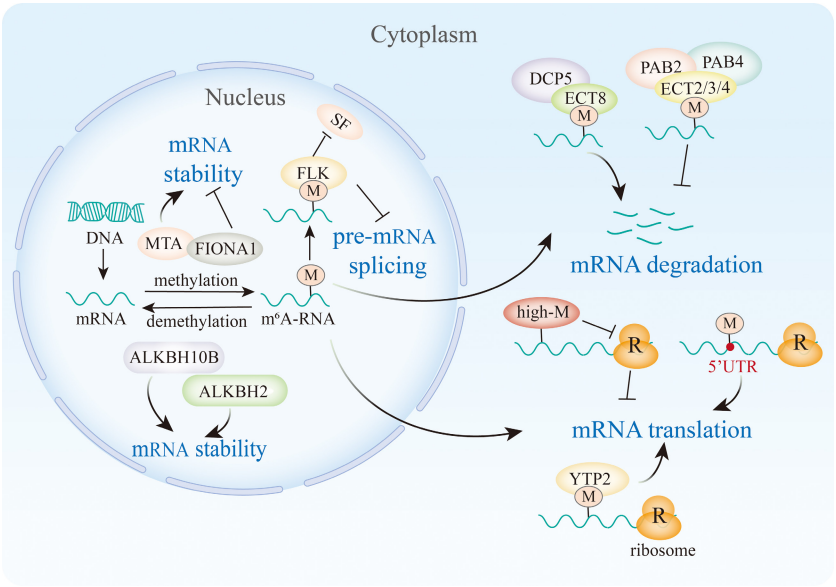

Fig. 2 m^{6}A modification affects the mRNA stability, splicing, and translation efficiency. In the nucleus, MTA, ALKBH10B, and ALKBH2 promote the mRNA stability, but FIONA1 inhibits the mRNA stability, and FLK recognizes the m^{6}A and inhibits the interaction with SF, thereby inhibiting the pre-mRNA splicing. In cytoplasm, the reader ECT8 recognizes the m^{6}A and interacts with DCP5 to promote the mRNA degradation. And m^{6}A readers ECT2/3/4 redundantly recruit PAB2 and PAB4 to protect the poly(A) tail from deadenylation. In plants, a high level m^{6}A inhibit ribosomes from combining with mRNA, but the m^{6}A sites at 5'UTR and recognized by YTP2 will promote the mRNA translation.

and *AREB1*[28,36]. What's more, m^{6}A writers MTA, MTB, and VIR are capable of regulating the salt and drought tolerance of plants by regulating the stability of mRNA[12,47]. The m^{6}A reader ECT2 enhances mRNA stability by influencing 3'UTR processing of transcripts[16]. Recently, a novel model reveals multiple m^{6}A readers ECT2/3/4 redundantly recruit PAB2 and PAB4, thereby protecting the m^{6}A-mediated mRNA poly(A) tail from deadenylation[48]. On the other hand, the interaction between different RNA modifications also can affect RNA stability, the interaction between YTHDF2 and m^{6}A is enhanced when HRSP12 binds to m^{1}A, which subsequently promotes intranuclear degradation mediated by the RNase P/MRP complex[49]. However, conventional biotechnological methods are unable to selectively modulate m^{6}A levels without altering gene structure or transcriptional activity. Recently, the novel CRISPR/dCas13a system can precisely add or eliminate m^{6}A modifications on particular RNA transcripts to investigate the impact of m^{6}A on mRNA stability[50]. In summary, the findings demonstrate that m^{6}A modification exerts distinct regulatory roles in mRNA stability within plants.

Translation efficiency of mRNA

Research in mammals has demonstrated that m^{6}A modifications that focus on the 5'UTR facilitate the direct interaction of m^{6}A-modified mRNA with ribosomes, enabling cap-independent translation, and initial support for this mechanism emerged from investigations into heat shock stress responses[51]. Moreover, the intricate interplay among distinct m^{6}A readers exerts profound regulatory effects on mRNA translational efficiency. For example, YTHDF3 acts synergistically with YTHDF1 to potentiate the latter's capacity to enhance mRNA translation. However there are few reports that m^{6}A modification directly affects m^{6}A-mRNA translation in plants. Excessive modification of m^{6}A on transcripts negatively affects the translation state, while modification near the start codon enhances translation, which seems to be due to the hypermethylation of transcripts inhibiting the synthesis of ribosomes or inhibiting mRNA loading into ribosomes[52]. While, in maize (*Zea mays* L.), researchers found that m^{6}A modification near the start codon can promote mRNA and ribosome binding, and then positively regulate mRNA translation efficiency. Recent advances in high-throughput sequencing technologies, particularly m^{6}A-seq and ribosome profiling (Ribo-seq), have enabled comprehensive investigations into the regulatory roles of m^{6}A modifications in plant translation efficiency. For instance, *MdMTA* positively regulates the m^{6}A modification and translation efficiency on the 5'UTR mRNA of *Md4CL3* to improve the drought tolerance of apples[12]. Similarly, MhYTP2 binds m^{6}A-modified *MdGDH1L* mRNA to enhance its translational efficiency, thereby increasing apple resistance to powdery mildew[53]. In strawberries, the researchers also found that m^{6}A modifications affect the expression of translation initiation factors, and positively regulate the translation efficiency of certain ABA pathway genes.

Splicing of mRNA

Alternative splicing is the process of pre-mRNA intron excision and exon linking to form mature mRNA with different functions. A number of studies have brought to light the abundance of m^{6}A in the exon of alternative splicing is more obvious than that of the intron, and the gene expression and splicing pattern are significantly changed after methyltransferase silencing. m^{6}A can impact the stability of transcription splicing sites by changing the secondary structure of RNA or directly acting on the spliceosome to regulate RNA differential splicing. The splicing difference caused by m^{6}A modification has a more significant regulation of flowering time. Some recent studies have indicated that m^{6}A-related proteins FLK and FIO1 influence the flowering of *Arabidopsis* by affecting the splicing of the key floral repressor FLC (FLOWERING LOCUS C)[54]. FLK, an m^{6}A-binding protein, binds to the FLC 3'UTR and limits FLC levels by inhibiting splicing and reducing its stability. What's more, mutants of the *Arabidopsis fio1* display aberrant splicing patterns[55]. In *Arabidopsis*, m^{6}A not only modulates mRNA splicing but is also found in pri-miRNAs, the absence of m^{6}A in pri-miRNAs within *mta*-mutated plants leads to reduced processing efficiency of pri-miRNAs, ultimately causing a decline in miRNA production[56].

m^{6}A is involved in plant development

In recent years, by analyzing the overall level of m^{6}A, researchers have found that m^{6}A modifications are widely present in plant mRNA and show dynamic changes during plant growth[56]. With the in-depth analysis of the function of m^{6}A in plants, it is known that m^{6}A modification takes place in roots, stems[28], leaves, flowers, fruits, and seeds to regulate their development (Fig. 3). However, research on m^{6}A in plants, particularly in major crops like wheat, rice, corn, and rapeseed (*Brassica napus* L.) lags behind that in animals and requires further exploration to elucidate its potential biological functions.

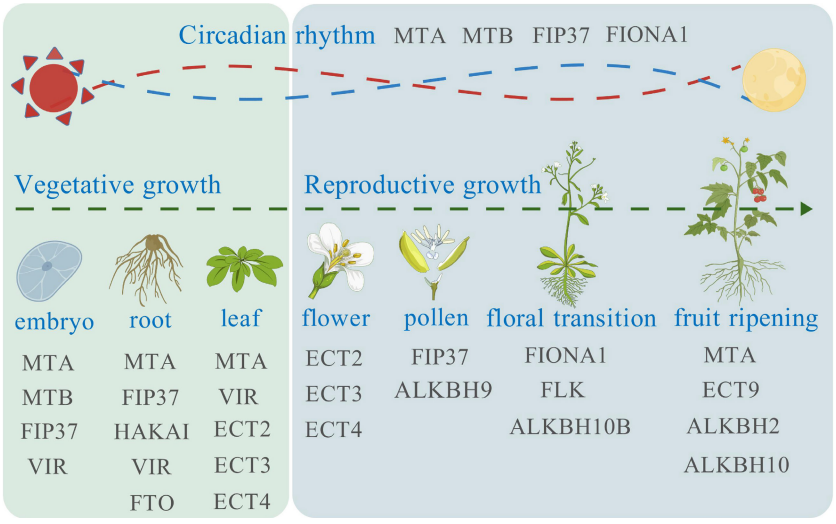

Fig. 3 m^{6}A modification affects plant development. During the plant vegetative growth, m^{6}A related proteins affect the embryo, root, and leaf formation. During the reproductive growth, m^{6}A related proteins affect the flower and pollen development, floral transition, and fruit ripening. The plant circadian rhythm is also affected by MTA, MTB, FIP37, and FIONA1.

m^{6}A affects plant tissue and organ development

That m^{6}A affects plant tissue and organ development has been mainly elucidated through the study of mutants with m^{6}A-related protein complexes. For instance, disrupting *Arabidopsis MTA* leads to developmental abnormalities such as an embryo-lethal phenotype and leaf morphological changes, and over-proliferation of shoot meristems. The replacement mutant (MTA-ABI3PROM:MTA) specifically expressing *mta* during embryonic development showed decreased apical dominance, floral organ malformation, increased epidermal branching, shortened root growth, abnormal root protoxylem development, and gravitropism defects[57]. What's more, the overexpression of the *PtrMTA* gene has been found to lead to a rise in the density of poplar trichomes[58]. In rice, deletion of *OsFIP* leads to early degradation of microspore in the vacuolar pollen stage, simultaneous abnormal meiosis in prophase I, and identified the 'UGWAMA' motif that is specifically modified by m^{6}A in rice panicles[30]. The virus-induced gene silencing (VIGS) mediated knockdown of *GhVIR* genes impacts the size, shape, and total number of leaf cells within cotton[59]. In the context of *Arabidopsis*, ECT2, ECT3, and ECT4 speed up organogenesis by stimulating cell division processes in organ primordia such as leaf morphology, flower development, and trichome branches[48]. Cadmium (Cd) stands as the most extensively distributed heavy-metal pollutant in soil. Under Cd stress, the m^{6}A methylation peaks throughout the soybean transcriptome elevate, when combined with rhizobia, these changes foster the growth of soybean roots[60]. In barley (*Hordeum vulgare* L.) roots, m^{6}A modification positively regulates genes involved in Cd response, and it is preferentially enriched in the vicinity of stop codons and within the 3'UTR[61]. Tomato contains nine YTH genes, among which *SlYTH1* exhibits the strongest expression. Knockout of *SlYTH1* can alleviate the inhibitory effect of exogenous GA3 on the root elongation of seedlings at a relatively low concentration[22].

m^{6}A is engaged in governing the flowering transition of plants

mRNA methylation and demethylation modifications exert significant functions in regulating floral transition. FIONA1 functions as an m^{6}A methyltransferase and also serves as a floral repressor, *fio1* mutants exhibit hypocotyl elongation and early flowering that are not dependent on photoperiod[29]. Multiple studies have revealed that FIONA1 modulates the floral transition by impacting the stability and splicing of *CO* and *SOC1*[62]. Additionally, FIONA1 influences RNA stability and alters the 3' end processing or splicing of *CCA1* and *LHY* transcripts to impact the circadian rhythm generator and photobiological behaviors. Furthermore, MTA, MTB, and FIP37 are also involved in regulating the plant circadian clock[63]. FLK, an m^{6}A reader discovered recently, explicitly links up with the m^{6}A site located in the 3'UTR of FLC mRNA, impacting floral transition through decreasing *FLC* stability and splicing[39]. Similarly, *FPA* (homolog of RBM15/15B) regulates flowering via the chromatin silencing pathway of *FLC*[64]. ALKBH10B functions as an m^{6}A mRNA demethylase, mutations of it result in elevated levels of m^{6}A in polyA RNA and reduce *SPL* mRNA accumulation, thus prolonging plastid staining and delaying the transition of *Arabidopsis* flowering period[17]. The above findings suggest that regulation of the floral transition is achieved through m^{6}A modification.

m^{6}A affects the expansion, ripening, and senescence of plant fruits

Varied m^{6}A methylation patterns across fruit development stages indicate modulation of m^{6}A writers' and erasers' expression and activity based on fruit developmental stages. A study showed that DNA methylation, specifically 5-methylcytosine (5mC) epigenetic modification, is crucial for controlling fruit ripening. Knocking out the SlDML2 (DNA demethylase) results in extensive DNA hypermethylation and significant suppression of fruit maturation. Likewise, the m^{6}A demethyltransferase SlALKBH2 not only controls m^{6}A modification but also influences DNA methylation to delay tomato fruit ripening[65]. Unlike tomato, kiwifruit ripening involves reader proteins, with AcALKBH10 and AcECT9 affecting the key determinants of fruit quality, including soluble sugars, and organic acids[18]. Recent findings showed a general positive correlation between m^{6}A and mRNA levels as tomato change from the immature green to ripening. Likewise, a positive tendency was observed between m^{6}A modification and strawberry fruit maturity, with the methyltransferase MTA boosting mRNA stability of two ABA pathway genes that impact the ripening process[36]. Cell expansion in fruit is primarily driven by phytohormones like auxin and gibberellic acid, as well as endoreduplication. A wealth of studies indicate that a multitude of genes related to hormone signaling pathways and endoreduplication undergo m^{6}A modification in *Arabidopsis*, maize, and tomato. What's more, dark stress triggers senescence in plants, leading to reduced total biomass and yield, and multiple studies have demonstrated that m^{6}A modification of transcripts associated with senescence can directly or indirectly modulate this process. Moreover, Sheikh et al. detected that the augmented degree of senescence in *Arabidopsis mta* mutants in the absence of light is attributed to elevated m^{6}A levels. This increase in m^{6}A levels activates senescence-related transcripts such as SAG21 through the action of NAP and NYE1, resulting in accelerated leaf deterioration[66]. These findings highlight the strong association between m^{6}A modification and the control of fruit growth, ripening, and aging processes. Given the interconnected nature of fruit ripening and senescence, investigating the impact of m^{6}A on both general and stress-induced senescence in crop plants holds promise for future research.

m^{6}A roles in plant-virus interaction

Plant survival and reproduction face challenges from fungal and bacterial diseases, known as biotic stresses. Viruses, as intracellular pathogens, hijack cells to replicate by utilizing their genetic material. In 1975, the m^{6}A modification in viral mRNAs was first spotted in simian virus 40 mRNAs[67]. This modification is characterized by its reversible nature, playing a significant role in altering both host and viral RNA (Table 1).

m^{6}A methylation exhibits a dual function in the context of plant virus infections. On the one hand, the RNA of numerous plant viruses contains m^{6}A modifications and this process influences RNA stability and the assembly of viral particles, ultimately modulating the effectiveness of viral infiltration. For instance, there are 2~4 m^{6}A modification sites on the transcript of potato Y virus (PVY) RNA, which silence plant demethylase genes and are conducive to virus infection[68]. Alfalfa mosaic virus (AMV) is a plant virus and it was found that the coat protein (CP) of AMV could interact specifically with AtALKBH9B to facilitate viral infection, however, the enhanced resistance to AMV resistance observed in the *alkbh9b* mutant could be replenished by mutations of *ECT2/3/5*[69]. Additionally, the MTB functions to positively regulate the infection of wheat yellow mosaic virus (WYMV) by means of stabilizing the viral RNA[70]. Through the dynamic regulation of methyltransferase and demethylase, the m^{6}A is finally recognized by the readers, which affects the stability of viral RNA by recruiting proteins associated with RNA degradation. The m^{6}A reader ECT2 recognizes the m^{6}A modification of the PepMV and interacts with the RNA degradation related proteins UPF3 and SMG7 to degrade the virus[71]. With further exploration into the m^{6}A modification, it is found that its regulation of RNA is complex and diverse. m^{6}A is an important molecular marker to distinguish host

Table 1. m^{6}A-related proteins in virus infects plants.

Virus name	Host	m^{6}A-related proteins	Ref.
Potato virus Y (PVY)	Tobacco	ALKBH9	[68]
Wheat yellow mosaic virus (WYMV)	Wheat	MTB	[70]
Pepino mosaic virus (PepMV)	Tomato	MTA/HAKAI/ECT2	[71]
Tobacco mosaic virus (TMV)	Tobacco	ALKBH5	[74]
Cucumber green mottle mosaic virus (CGMMV)	Watermelon	ALKBH2B/ALKBH4B	[75]
Bacterial wilt (BW)	Peanut	ALKBH15	[76]
Powdery mildew (PM)	Apple	MhYTP2	[77]
Alfalfa mosaic viral (AMV)	*Arabidopsis*	ALKBH9B	[78]
Plum pox virus (PPV)	Tobacco	ALKBH9	[79]

cells from foreign nucleic acids. Studies have shown that partial viruses have evolved to use the m^{6}A modification system to evade host monitoring of foreign nucleic acids, after some virus RNA is modified by m^{6}A, it is more advantageous to escape host recognition. For example, Lu et al. revealed that HMPV acquires m^{6}A modifications on its RNA as an evolutionary strategy to mimic cellular RNAs, thereby evading detection by the host innate immune system. However, research in plant viruses remains significantly underdeveloped compared to mammalian systems[72]. Future studies should elucidate how m^{6}A modifications mediate immune evasion in plant-virus interactions.

Infections caused by viruses are capable of altering the m^{6}A levels within the host, potentially influencing virus infection dynamics[73]. Research has demonstrated that TMV (Tobacco mosaic virus) infection reduces endogenous gene m^{6}A levels by 40% by the 21st day in tobacco[74]. Upon CGMMV infection, the *ALKBH4B* in watermelon exhibited a significant increase and 59 modified genes related to plant immunity notably decreased[75]. Conversely, exposure of *Arabidopsis* to AMV (alfalfa mosaic virus) infection causes m^{6}A levels to go up. In addition, after rice was infected by rice stripe virus (RSV), the zenith of m^{6}A modification associated with the regulation of RNA silencing pathways of major antiviral-related genes in rice was increased by MeRIP sequencing[14]. Multi-omics analysis of m^{6}A indicated that the m^{6}A demethylase ALKBH15 removes m^{6}A modification from *Rx_N* gene, leading to increased resistance to peanut bacterial wilt (BW)[76]. The above studies have clearly shown that virus infection can regulate the m^{6}A modification level of plant endogenous genes. However, the specific mechanism of the increase or decrease of the level of m^{6}A in the process of virus infection needs to be further studied. Guo et al. illustrated that MhYTP2's m^{6}A binding capability regulates PM resistance by promoting the translation efficiency of antioxidant genes[77]. These investigations reveal that plant viruses can be modified by methyltransferase complex m^{6}A after infecting the host. Furthermore, viral infection disrupts the m^{6}A modifications of endogenous plant genes. During the evolution of plant viruses, certain viruses have developed proteins with demethylase-like structures to adapt to the host environment.

m^{6}A roles in abiotic stress response in plant

Plants often encounter a wide range of environmental challenges during their growth and development. These challenges can significantly impact their survival and productivity. Some of the most common stress factors include salt, heat, cold, and drought, each presenting unique difficulties for plants. However, growing evidence suggests that m^{6}A levels and sites are involved in dynamically regulating the response to these abiotic stresses (Fig. 4).

Response to temperature stress

The m^{6}A has been observed to respond to low and high temperature stress in crop growth. For instance, cold treatment in *Arabidopsis* leads to the misregulation of translation efficacy in approximately a third of the genomic genes[80]. Notably, several studies have shown that AtMTA affects photosynthetic efficiency under low temperatures. What's more, the downregulation of *Arabidopsis fip37* affects the translation of cytoplasmic transcripts associated with photosynthesis under cold conditions, indicating the existence of m^{6}A-dependent translational regulation of chloroplast function[81]. The newly identified m^{6}A-binding protein MhYTP2 interacts with the low-temperature response associated RNA helicase MdRH20 and the cold-shock protein MdGRP2 in apple, leading to enhanced cold resistance. Furthermore, in tomato, an analysis of the RNA methylome disclosed that transcripts with enhanced m^{6}A levels under MLT (moderate low temperature) stress were predominantly associated with ATP-binding pathways, which causes an elevation in the ABA content inside the anthers and impairs the formation of the pollen wall[82]. m^{6}A writers (FIP37/VIR/HAKAI) were significantly upregulated by heat stress in tomato[83]. Similarly, m^{6}A methylase mutants *vir* and *hakai* in *Arabidopsis* seedlings exhibit sensitivity to

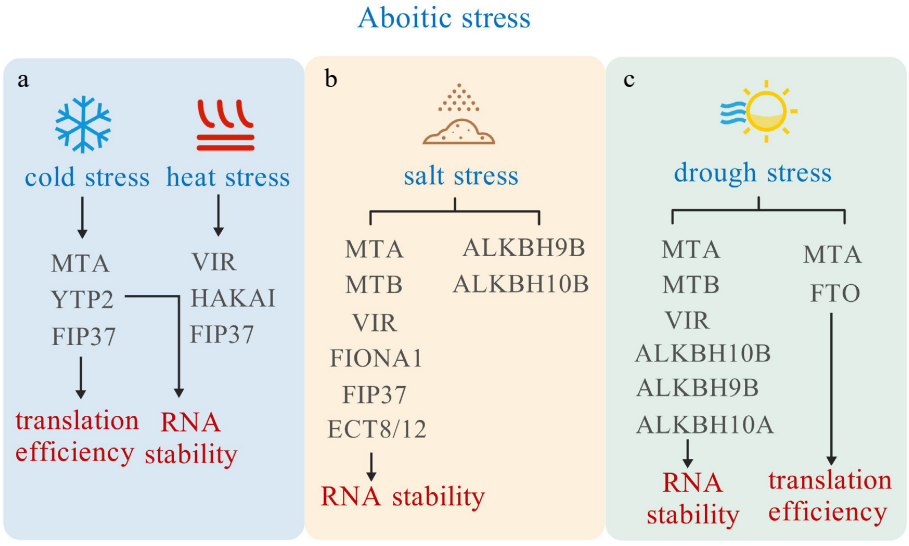

Fig. 4 m^{6}A modification role in responding to abiotic stresses. m^{6}A related proteins influence the mRNA stability and translation efficiency, thereby responding to cold, heat, salt, and drought stress.

heat stress, resulting in significant differential expression of most heat-related genes during stress and recovery. Apart from having an impact on m^{6}A-associated proteins, temperature stress is capable of altering the distribution pattern of m^{6}A. Under low-temperature stress, there is a more substantial deposition of m^{6}A within the 5'UTR in highly cold-resistant *Brassica rapa*. This deposition actively participates in the cold resistance mechanism by modulating the expression levels of mRNA[84]. Liu et al. probed into the effect of elevated temperature stress on Pak-choi, and their findings indicated an obvious correlation between m^{6}A and transcript expression, with the predominant m^{6}A enrichment zone in cabbage being the 3'UTR[9].

Response to salt stress

Salt stress, also known as salinity stress, comes about when salts accumulate to an excessive degree in the soil. This can disrupt the plant's ability to absorb water and essential nutrients. Research in *Arabidopsis* has shown that m^{6}A modification typically exhibits a complex association with gene expression under salt stress. For instance, mutants of the m^{6}A writer components, such as *mta*, *mtb*, *vir*, *fiona1*[85], and *fip37*[76] exhibited salt-sensitive phenotypes. Specifically, *Arabidopsis* VIR-mediated increases in m^{6}A modification levels by affecting mRNA stability or 3'UTR length to enhance plant salt tolerance[86]. The m^{6}A mediated by ATALKBH10B influences germination and seedling survival rates by boosting the stability of salt stress-responsive genes. What's more, ECT8 directly interacts with the decapping protein to promote the breakdown of transcripts encoding negative regulators of salt stress responses[80]. Meanwhile, the *Arabidopsis* mutant of *ect12* also exhibited sensitivity to salt[33]. In addition to *Arabidopsis*, the relationship between m^{6}A methylated protein and salt stress has also been reported in other crops and ligneous plants. Wang et al. employed MeRIP-seq methodology to analyze rice buds and roots subjected to salt stress, revealing a pronounced enrichment of m^{6}A modification near the initiation and termination codons. Furthermore, the salt stress conditions led to a notable decrease in the expression of *OsMTA2* in roots and *OsVIR* in buds[87]. In sorghum (*Sorghum bicolor*), the overexpression of *SbMTA* increases the m^{6}A level and salt tolerance, whereas the overexpression of the m^{6}A eraser *SbALKBH10B* exhibits an opposite phenotype[88]. Currently, the relationship between the ALKBH family and plant salt resistance has been relatively well-studied. For example, reducing the expression levels of *GhALKBH10* in cotton, and *SlALKBH10B* in tomato can enhance salt tolerance by increasing the m^{6}A level[7,89]. However, overexpressing *PvALKBH10_N* in switchgrass (*Panicum virgatum*)[90], *BvALKBH10B* in sugar beet (*Beta vulgaris*)[91], and *PagALKBH9B* and *PagALKBH10B* in *poplar*[92] can enhance the plants' salt tolerance by decreasing the m^{6}A level. These findings suggest significant alterations in m^{6}A modification as an answer to the challenge of salt stress.

Response to drought stress

The capabilities of m^{6}A writers, readers, and erasers have been observed to act in the face of drought stress in certain species. A case in point is that MTA boosts drought tolerance by influencing trichome and root elaboration, oxidative stress, and lignin deposition[93]. Heterologous expression of watermelon *ClMTB* in tobacco can affect the stability of drought tolerance-related gene transcripts and improve drought resistance[75]. Not all m^{6}A writers in plants confer benefits in enhancing plant drought stress resistance. In rice, the expression levels of *OsMTA*, *OsMTB*, and *OsVIR* m^{6}A writers were reduced under drought conditions. Moreover, heterologous expression of the human RNA demethylase gene *FTO* in rice promotes root meristem cell proliferation and enhances drought tolerance[46]. Similarly, under drought conditions, maize demethylase genes *ALKBH10A/10B*, as well as sea-buckthorn demethylase genes *HrALKBH10B/10C/10D*, showed significant upregulation. These findings suggest that plants may modulate their response to drought stress by decreasing m^{6}A levels. However, the expression levels of *ALKBH6/8B/10A* in rice were down-regulated due to drought stress[93]. Additionally, characterization of m^{6}A methylation under drought stress reveals that the m^{6}A reader SiYTH1 mediates drought tolerance by stabilizing m^{6}A-modified transcripts involved in ROS elimination[94]. In the future, studies should deeper elucidate the molecular mechanisms of how m^{6}A-related proteins mediate drought resistance.

Outlooks, perspectives, and future research direction

Although there has been remarkable progress in deciphering m^{6}A's biological roles, numerous unresolved questions and undiscovered regulatory dimensions remain to be explored. Firstly, current research on the roles of m^{6}A modifications in plants have primarily focused on nuclear transcriptomes, while the characteristics and biological functions of m^{6}A modifications in chloroplast and mitochondrial transcriptomes remain largely unexplored. For instance, Wang et al. showed that the global m^{6}A methylation levels in chloroplasts and mitochondria are significantly higher than in the nucleus. While the methylation patterns of rRNAs and tRNAs in these organelles resemble nuclear patterns, distinct differences are observed in mRNA methylation profiles[95]. Intriguingly, a high abundance of m^{6}A modifications in maize mitochondria shows a negative correlation with translational efficiency[52]. These findings suggest that the mechanisms governing m^{6}A modification in chloroplasts and mitochondria require further investigation. Secondly, although the functional significance of m^{6}A in plant growth and development is being rapidly uncovered, how m^{6}A cooperates with other epigenetic modifications to regulate these processes remains poorly understood. While, recent work in maize has uncovered a functional crosstalk between m^{6}A and DNA 5-methylcytosine (5mC), demonstrating that the m^{6}A methyltransferase ZmMTA associates with the chromatin remodeler ZmDDM1 to coordinately regulate maize kernel development[96]. Treatment with the RNA methylation inhibitor (DZnepA) and the DNA methylation inhibitor (5-azaC) in moso bamboo (*Phyllostachys edulis*) leads to an increase in lateral roots, thereby interfering with the normal development of the root system[97]. Beyond DNA modifications, histone modifications warrant equal investigative priority in m^{6}A studies. For example, when the H3K36me3 (Histone H3 lysine 36 trimethylation) methyltransferase *SETD2* was depleted or the demethylase *KDM4A* was upregulated, it led to a considerable decline of m^{6}A modification in both humans and mice (*Mus musculus*)[85]. Future research must prioritize a more comprehensive exploration of how diverse epigenetic modifications influence plant growth. Thirdly, to date, rare experimental evidence has demonstrated that viral proteins can directly remove m^{6}A modifications *in vivo*. Although m^{6}A methylation represents one of the most abundant post-transcriptional modifications in viral RNAs and plays a crucial role in virus-host interactions, its precise regulatory mechanisms remain poorly characterized. Systematic investigation of the relationship between viral RNA methylation patterns and host immune recognition may unveil novel molecular strategies underlying viral pathogenesis. Fourth, in addition to modulating plant biological processes through mRNA metabolism regulation, RNA epigenetic modifications also play crucial roles in mediating protein-RNA interactions in plants. For example, a recent study demonstrated that MTA mediates m^{6}A deposition at the 3'UTR of the natural antisense transcript (as-NIA1), which facilitates the PTB3-as-NIA1 interaction to stabilize NIA1

mRNA, thereby regulating NO biosynthesis and stomatal movement[98]. Future investigations into how diverse RNA modifications regulate protein-RNA interactions will significantly advance our mechanistic understanding of plant growth and developmental processes.

The detection of m^{6}A modification is essential for elucidating its biological functions in plants. The introduction of MeRIP-seq in 2012 marked a breakthrough in m^{6}A research, catalyzing an era of rapid technological development. Current advances in sequencing technology focus on two primary goals: reducing RNA input and improving modification resolution, as evidenced by emerging methods like picoMeRIP-seq and m^{6}A-SAC-seq[99,100]. Furthermore, when integrated with plant single-cell transcriptomics and spatial transcriptomics advancements, m^{6}A modification detection technology could enhance the detailed investigation of plant RNA transcriptional regulation. Deciphering the biological functions of m^{6}A is fundamental to unraveling its profound influence on plant development and adaptation. In the future, elucidating the regulatory networks of m^{6}A in plants not only holds significant potential for enhancing crop yield and stress tolerance but may also provide novel molecular targets for precision breeding strategies.

Ethical statements

Not applicable.

Author contributions

The authors confirm contribution to the paper as follows: study conception and design: Shi Y, Yang S; draft manuscript preparation: Shi Y, Yang S, Pei T, Xu Y; data collection: Zhao Y, Xue H, Ma X. All authors reviewed the results and approved the final version of the manuscript.

Data availability

The images included in this review are original. All data generated or analyzed during this study are included in this published article and further information can be obtained from the corresponding author upon reasonable request.

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Conflict of interest

The authors declare that they have no conflict of interest.

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References

1. Du J, Johnson LM, Jacobsen SE, Patel DJ. 2015. DNA methylation pathways and their crosstalk with histone methylation. *Nature Reviews Molecular Cell Biology* 16:519–32
2. Meyer KD, Jaffrey SR. 2014. The dynamic epitranscriptome: N^6-methyladenosine and gene expression control. *Nature Reviews Molecular Cell Biology* 15:313–26
3. Ramakrishnan M, Rajan KS, Mullasseri S, Palakkal S, Kalpana K, et al. 2022. The plant epitranscriptome: revisiting pseudouridine and 2'-O-methyl RNA modifications. *Plant Biotechnology Journal* 20:1241–56
4. Chmielowska-Bąk J, Arasimowicz-Jelonek M, Deckert J. 2019. In search of the mRNA modification landscape in plants. *BMC Plant Biol* 19:421
5. Luo GZ, MacQueen A, Zheng G, Duan H, Dore LC, et al. 2014. Unique features of the m^{6}A methylome in *Arabidopsis thaliana*. *Nature Communications* 5:5630
6. Wang G, Li H, Ye C, He K, Liu S, et al. 2024. Quantitative profiling of m^{6}A at single base resolution across the life cycle of rice and *Arabidopsis*. *Nature Communications* 15:4881
7. Cui C, Ma Z, Wan H, Gao J, Zhou B. 2022. GhALKBH10 negatively regulates salt tolerance in cotton. *Plant Physiology and Biochemistry* 192:87–100
8. Liu P, Liu H, Zhao J, Yang T, Guo S, et al. 2024. Genome-wide identification and functional analysis of mRNA m^{6}A writers in soybean under abiotic stress. *Frontiers in Plant Science* 15:1446591
9. Liu G, Wang J, Hou X. 2020. Transcriptome-wide *N*^{6}-methyladenosine (m^{6}A) methylome profiling of heat stress in Pak-choi (*Brassica rapa* ssp. *chinensis). Plants* 9:1080
10. Meyer KD, Saletore Y, Zumbo P, Elemento O, Mason CE, et al. 2012. Comprehensive analysis of mRNA methylation reveals enrichment in 3' UTRs and near stop codons. *Cell* 149:1635–46
11. Huang T, He WJ, Li C, Zhang JB, Liao YC, et al. 2022. Transcriptome-wide analyses of RNA m^{6}A methylation in hexaploid wheat reveal its roles in mRNA translation regulation. *Frontiers in Plant Science* 13:917335
12. Hou N, Li C, He J, Liu Y, Yu S, et al. 2022. MdMTA-mediated m^{6}A modification enhances drought tolerance by promoting mRNA stability and translation efficiency of genes involved in lignin deposition and oxidative stress. *New Phytologist* 234:1294–314
13. Deng H, Cheema J, Zhang H, Woolfenden H, Norris M, et al. 2018. Rice *in vivo* RNA structurome reveals RNA secondary structure conservation and divergence in plants. *Molecular Plant* 11:607–22
14. Zhang TY, Wang ZQ, Hu HC, Chen ZQ, Liu P, et al. 2021. Transcriptome-wide *N*^{6}-methyladenosine (m^{6}A) profiling of susceptible and resistant wheat varieties reveals the involvement of variety-specific m^{6}A modification involved in virus-host interaction pathways. *Frontiers in Microbiology* 12:656302
15. Xu X, Zhang C, Xu X, Cai R, Guan Q, et al. 2023. Riboflavin mediates m^{6}A modification targeted by miR408, promoting early somatic embryogenesis in longan. *Plant Physiology* 192:1799–820
16. Wei LH, Song P, Wang Y, Lu Z, Tang Q, et al. 2018. The m^{6}A reader ECT2 controls trichome morphology by affecting mRNA stability in *Arabidopsis*. *The Plant Cell* 30:968–85
17. Duan HC, Wei LH, Zhang C, Wang Y, Chen L, et al. 2017. ALKBH10B is an RNA *N*^{6}-methyladenosine demethylase affecting *Arabidopsis* floral transition. *The Plant Cell* 29:2995–3011
18. Su D, Shu P, Hu N, Chen Y, Wu Y, et al. 2024. Dynamic m^{6}A mRNA methylation reveals the involvement of AcALKBH10 in ripening-related quality regulation in kiwifruit. *New Phytologist* 243:2265–78
19. Yue J, Wei Y, Zhao M. 2022. The reversible methylation of m6A is involved in plant virus infection. *Biology* 11:271
20. Shi H, Wei J, He C. 2019. Where, when, and how: context-dependent functions of RNA methylatIon writers, readers, and erasers. *Molecular Cell* 74:640–50
21. Kumari P, Bhattacharjee S, Venkat Raman K, Tilgam J, Paul K, et al. 2025. Identification of *methyltransferase* and demethylase genes and their expression profiling under biotic and abiotic stress in pigeon pea (*Cajanus cajan* [L.] Millspaugh). *Frontiers in Plant Science* 15:1521758
22. Yin S, Ao Q, Qiu T, Tan C, Tu Y, et al. 2022. Tomato SlYTH1 encoding a putative RNA m^{6}A reader affects plant growth and fruit shape. *Plant Science* 323:111417
23. Bokar JA, Rath-Shambaugh ME, Ludwiczak R, Narayan P, Rottman F. 1994. Characterization and partial purification of mRNA *N*^{6}-adenosine methyltransferase from HeLa cell nuclei. Internal mRNA methylation requires a multisubunit complex. *Journal of Biological Chemistry* 269:17697–704

24. Růžička K, Zhang M, Campilho A, Bodi Z, Kashif M, et al. 2017. Identification of factors required for m^{6}A mRNA methylation in *Arabidopsis* reveals a role for the conserved E3 ubiquitin ligase HAKAI. *New Phytologist* 215:157–72
25. Zhang M, Bodi Z, Mackinnon K, Zhong S, Archer N, et al. 2022. Two zinc finger proteins with functions in m^{6}A writing interact with HAKAI. *Nature Communications* 13:1127
26. Zhong S, Li H, Bodi Z, Button J, Vespa L, et al. 2008. MTA is an *Arabidopsis* messenger RNA adenosine methylase and interacts with a homolog of a sex-specific splicing factor. *The Plant Cell* 20:1278–88
27. Ping XL, Sun BF, Wang L, Xiao W, Yang X, et al. 2014. Mammalian WTAP is a regulatory subunit of the RNA N6-methyladenosine methyltransferase. *Cell Res* 24:177–89
28. Shen L, Liang Z, Gu X, Chen Y, Teo ZWN, et al. 2016. *N*^{6}-methyladenosine RNA modification regulates shoot stem cell fate in *Arabidopsis*. *Developmental Cell* 38:186–200
29. Wang C, Yang J, Song P, Zhang W, Lu Q, et al. 2022. FIONA1 is an RNA *N*^{6}-methyladenosine methyltransferase affecting *Arabidopsis* photomorphogenesis and flowering. *Genome Biology* 23:40
30. Zhang F, Zhang YC, Liao JY, Yu Y, Zhou YF, et al. 2019. The subunit of RNA *N*^{6}-methyladenosine methyltransferase OsFIP regulates early degeneration of microspores in rice. *PLoS Genetics* 15:e1008120
31. Du H, Zhao Y, He J, Zhang Y, Xi H, et al. 2016. YTHDF2 destabilizes m^{6}A-containing RNA through direct recruitment of the CCR4-NOT deadenylase complex. *Nature Communication* 7:12626
32. Ma W, Cui S, Lu Z, Yan X, Cai L, et al. 2022. YTH domain proteins play an essential role in rice growth and stress response. *Plants* 11:2206
33. Amara U, Hu J, Park SJ, Kang H. 2024. ECT12, an YTH-domain protein, is a potential mRNA m^{6}A reader that affects abiotic stress responses by modulating mRNA stability in *Arabidopsis*. *Physiology and Biochemistry* 206:108255
34. Song P, Yang J, Wang C, Lu Q, Shi L, et al. 2021. *Arabidopsis N*^{6}-methyladenosine reader CPSF30-L recognizes FUE signals to control polyadenylation site choice in liquid-like nuclear bodies. *Molecular Plant* 14:571–87
35. Arribas-Hernández L, Bressendorff S, Hansen MH, Poulsen C, Erdmann S, et al. 2018. An m^{6}A-YTH module controls developmental timing and morphogenesis in *Arabidopsis*. *The Plant Cell* 30:952–67
36. Zhou L, Tang R, Li X, Tian S, Li B, et al. 2021. *N*^{6}-methyladenosine RNA modification regulates strawberry fruit ripening in an ABA-dependent manner. *Genome Biology* 22:168
37. Wu J, Peled-Zehavi H, Galili G. 2020. The m^{6}A reader ECT2 post-transcriptionally regulates proteasome activity in *Arabidopsis*. *New Phytologist* 228:151–62
38. Nguyen TKH, Amara U, Kang H. 2025. ECT8, an mRNA m^{6}A reader, enhances salt stress tolerance by modulating mRNA stability in *Arabidopsis*. *Physiologia Plantarum* 177:e70135
39. Amara U, Hu J, Cai J, Kang H. 2023. FLK is an mRNA m^{6}A reader that regulates floral transition by modulating the stability and splicing of FLC in *Arabidopsis*. *Molecular Plant* 16:919–29
40. Jia G, Fu Y, Zhao X, Dai Q, Zheng G, et al. 2011. *N*^{6}-methyladenosine in nuclear RNA is a major substrate of the obesity-associated FTO. *Nature Chemical Biology* 7:885–87
41. Amara U, Shoaib Y, Kang H. 2022. ALKBH9C, a potential RNA m^{6}A demethylase, regulates the response of *Arabidopsis* to abiotic stresses and abscisic acid. *Plant, Cell & Environment* 45:3566–81
42. Huong TT, Ngoc LNT, Kang H. 2020. Functional characterization of a putative RNA demethylase ALKBH6 in *Arabidopsis* growth and abiotic stress responses. *International Journal of Molecular Sciences* 21:6707
43. 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 Biology* 20:156
44. Li B, Zhang M, Sun W, Yue D, Ma Y, et al. 2023. *N*^{6}-methyladenosine RNA modification regulates cotton drought response in a Ca^{2+} and ABA-dependent manner. *Plant Biotechnology Journal* 21:1270–85
45. Chen M, Urs MJ, Sánchez-González I, Olayioye MA, Herde M, et al. 2018. m^{6}A RNA degradation products are catabolized by an evolutionarily conserved *N*^{6}-Methyl-AMP deaminase in plant and mammalian cells. *The Plant Cell* 30:1511–22
46. Yu Q, Liu S, Yu L, Xiao Y, Zhang S, et al. 2021. RNA demethylation increases the yield and biomass of rice and potato plants in field trials. *Nature Biotechnology* 39:1581–88
47. Anderson SJ, Kramer MC, Gosai SJ, Yu X, Vandivier LE, et al. 2018. *N*^{6}-methyladenosine inhibits local ribonucleolytic cleavage to stabilize mRNAs in *Arabidopsis*. *Cell Reports* 25:1146–1157.e3
48. Song P, Wei L, Chen Z, Cai Z, Lu Q, et al. 2023. m^{6}A readers ECT2/ECT3/ECT4 enhance mRNA stability through direct recruitment of the poly(A) binding proteins in *Arabidopsis*. *Genome Biology* 24:103
49. Boo SH, Ha H, Kim YK. 2022. m^{1}A and m^{6}A modifications function cooperatively to facilitate rapid mRNA degradation. *Cell Reports* 40:111317
50. Shi C, Zou W, Liu X, Zhang H, Li X, et al. 2024. Programmable RNA *N*^{6}-methyladenosine editing with CRISPR/dCas13a in plants. *Plant Biotechnology Journal* 22:1867–80
51. Coots RA, Liu XM, Mao Y, Dong L, Zhou J, et al. 2017. m^{6}A facilitates eIF4F-independent mRNA translation. *Molecular Cell* 68:504–514.e7
52. Luo JH, Wang Y, Wang M, Zhang LY, Peng HR, et al. 2020. Natural variation in RNA m^{6}A methylation and its relationship with translational status. *Plant Physiology* 182:332–44
53. Guo T, Yang Z, Bao R, Fu X, Wang N, et al. 2023. The m^{6}A reader MhYTP2 regulates the stability of its target mRNAs contributing to low nitrogen tolerance in apple (*Malus domestica*). *Horticulture Research* 10:uhad094
54. Cai J, Hu J, Amara U, Park SJ, Li Y, et al. 2023. *Arabidopsis N*^{6}-methyladenosine methyltransferase FIONA1 regulates floral transition by affecting the splicing of FLC and the stability of floral activators SPL3 and SEP3. *Journal of Experimental Botany* 74:864–77
55. Parker MT, Soanes BK, Kusakina J, Larrieu A, Knop K, et al. 2022. m^{6}A modification of U6 snRNA modulates usage of two major classes of pre-mRNA 5' splice site. *eLife* 11:e78808
56. Bhat SS, Bielewicz D, Gulanicz T, Bodi Z, Yu X, et al. 2020. mRNA adenosine methylase (MTA) deposits m^{6}A on pri-miRNAs to modulate miRNA biogenesis in *Arabidopsis thaliana*. *Proceedings of the National Academy of Sciences of the United States of America* 117:21785–95
57. Bodi Z, Zhong S, Mehra S, Song J, Graham N, et al. 2012. Adenosine methylation in *Arabidopsis* mRNA is sssociated with the 3' end and reduced levels cause developmental defects. *Frontiers in Plant Science* 3:48
58. Lu L, Zhang Y, He Q, Qi Z, Zhang G, et al. 2020. MTA, an RNA m^{6}A methyltransferase, enhances drought tolerance by regulating the development of trichomes and roots in poplar. *International Journal of Molecular Science* 21:2462
59. Huang X, Abuduwaili N, Wang X, Tao M, Wang X, Huang G. 2022. Cotton (*Gossypium hirsutum*) VIRMA as an *N*^{6}-methyladenosine RNA methylation regulator participates in controlling chloroplast-dependent and independent leaf development. *International Journal of Molecular Sciences* 23:9887
60. Han X, Wang J, Zhang Y, Kong Y, Dong H, et al. 2023. Changes in the m^{6}A RNA methylome accompany the promotion of soybean root growth by rhizobia under cadmium stress. *Journal of Hazardous Materials* 441:129843
61. Su T, Fu L, Kuang L, Chen D, Zhang G, et al. 2022. Transcriptome-wide m^{6}A methylation profile reveals regulatory networks in roots of barley under cadmium stress. *Journal of Hazardous Materials* 423:127140
62. Due Tankmar M, Reichel M, Arribas-Hernández L, Brodersen P. 2023. A YTHDF-PABP interaction is required for m^{6}A-mediated organogenesis in plants. *EMBO Reports* 24:e57741
63. Wang X, Jiang B, Gu L, Chen Y, Mora M, et al. 2021. A photoregulatory mechanism of the circadian clock in *Arabidopsis*. *Nature Plants* 7:1397–408
64. Lim MH, Kim J, Kim YS, Chung KS, Seo YH, et al. 2004. A new *Arabidopsis* gene, FLK, encodes an RNA binding protein with K homology motifs and regulates flowering time via FLOWERING LOCUS C. *The Plant Cell* 16:731–40
65. Tan T, Li Y, Tang B, Chen Y, Chen X, et al. 2022. Knockout of *SlALKBH2* weakens the DNA damage repair ability of tomato. *Plant Science* 319:111266
66. Sheikh AH, Tabassum N, Rawat A, Almeida Trapp M, Nawaz K, Hirt H. 2024. m^{6}A RNA methylation counteracts dark-induced leaf senescence in *Arabidopsis*. *Plant Physiology* 194:2663–78

67. Lavi S, Shatkin AJ. 1975. Methylated simian virus 40-specific RNA from nuclei and cytoplasm of infected BSC-1 cells. *Proceedings of the National Academy of Sciences of the United States of America* 72:2012–16
68. Yue J, Wei Y, Sun Z, Chen Y, Wei X, et al. 2022. AlkB RNA demethylase homologues and N^6-methyladenosine are involved in Potyvirus infection. *Molecular Plant Pathology* 23:1555–64
69. Martínez-Pérez M, Aparicio F, Arribas-Hernández L, Tankmar MD, Rennie S, et al. 2023. Plant YTHDF proteins are direct effectors of antiviral immunity against an N^6-methyladenosine-containing RNA virus. *EMBO Journal* 42:e113378
70. Zhang T, Shi C, Hu H, Zhang Z, Wang Z, et al. 2022. N^6-methyladenosine RNA modification promotes viral genomic RNA stability and infection. *Nature Communications* 13:6576
71. He H, Ge L, Chen Y, Zhao S, Li Z, et al. 2024. m^{6}A modification of plant virus enables host recognition by NMD factors in plants. *Science China Life Sciences* 67:161–74
72. Lu M, Zhang Z, Xue M, Zhao BS, Harder O, et al. 2020. N^6-methyladenosine modification enables viral RNA to escape recognition by RNA sensor RIG-I. *Nature Microbiology* 5:584–98
73. He M, Li Z, Xie X. 2023. The Roles of N^6-methyladenosine modification in plant-RNA virus interactions. *International Journal of Molecular Sciences* 24:15608
74. Li Z, Shi J, Yu L, Zhao X, Ran L, et al. 2018. N^6-methyl-adenosine level in *Nicotiana tabacum* is associated with tobacco mosaic virus. *Virology Journal* 15:87
75. He Y, Li L, Yao Y, Li Y, Zhang H, et al. 2021. Transcriptome-wide N^6-methyladenosine (m^{6}A) methylation in watermelon under CGMMV infection. *BMC Plant Biology* 21:516
76. Zhao K, Li Z, Ke Y, Ren R, Cao Z, et al. 2024. Dynamic N^6-methyladenosine RNA modification regulates peanut resistance to bacterial wilt. *New Phytologist* 242:231–46
77. Guo T, Liu C, Meng F, Hu L, Fu X, et al. 2022. The m^{6}A reader MhYTP2 regulates MdMLO19 mRNA stability and antioxidant genes translation efficiency conferring powdery mildew resistance in apple. *Plant Biotechnology Journal* 20:511–25
78. Alvarado-Marchena L, Martínez-Pérez M, Úbeda JR, Pallas V, Aparicio F. 2022. Impact of the potential m^{6}A modification sites at the 3'UTR of Alfalfa Mosaic Virus RNA3 in the viral infection. *Viruses* 14:1718
79. Yue J, Lu Y, Sun Z, Guo Y, León DS, et al. 2023. Methyltransferase-like (METTL) homologues participate in *Nicotiana benthamiana* antiviral responses. *Plant Signaling & Behavior* 18:2214760
80. Cai Z, Tang Q, Song P, Tian E, Yang J, et al. 2024. The m^{6}A reader ECT8 is an abiotic stress sensor that accelerates mRNA decay in *Arabidopsis*. *The Plant Cell* 36:2908–26
81. Vicente AM, Manavski N, Rohn PT, Schmid LM, Garcia-Molina A, et al. 2023. The plant cytosolic m^{6}A RNA methylome stabilizes photosynthesis in the cold. *Plant Communications* 4:100634
82. Yang D, Xu H, Liu Y, Li M, Ali M, et al. 2021. RNA N6-methyladenosine responds to low-temperature stress in tomato anthers. *Frontiers in Plant Science* 12:687826
83. Shen H, Luo B, Wang Y, Li J, Hu Z, et al. 2022. Genome-wide identification, classification and expression analysis of m^{6}A gene family in *Solanum lycopersicum*. *International Journal of Molecular Sciences* 23:4522
84. Ma L, Tao X, Fahim AM, Xu Y, Zhang Y, et al. 2025. Novel insights into the unique characterization of N^6-methyladenosine RNA modification and regulating cold tolerance in winter *Brassica rapa*. *International Journal of Biological Macromolecules* 303:140460
85. Cai J, Hu J, Xu T, Kang H. 2024. FIONA1-mediated mRNA m^{6}A methylation regulates the response of *Arabidopsis* to salt stress. *Plant, Cell & Environment* 47:900–12
86. Hu J, Cai J, Park SJ, Lee K, Li Y, et al. 2021. N^6 -methyladenosine mRNA methylation is important for salt stress tolerance in *Arabidopsis*. *Plant Journal* 106:1759–75
87. Wang Y, Du F, Li Y, Wang J, Zhao X, et al. 2022. Global N^6-methyladenosine profiling revealed the tissue-specific epitranscriptomic regulation of Rice responses to salt stress. *International Journal of Molecular Sciences* 23:2091
88. Zheng H, Dang Y, Gao Y, Li S, Wu F, et al. 2024. An mRNA methylase and demethylase regulate sorghum salt tolerance by mediating N^6-methyladenosine modification. *Plant Physiology* 196:3048–70
89. Shen H, Zhou Y, Liao C, Xie Q, Chen G, et al. 2024. The AlkB homolog SlALKBH10B negatively affects drought and salt tolerance in *Solanum lycopersicum*. *International Journal of Molecular Sciences* 25:173
90. Liu H, Lin M, Wang H, Li X, Zhou D, et al. 2024. N^6-methyladenosine analysis unveils key mechanisms underlying long-term salt stress tolerance in switchgrass (*Panicum virgatum*). *Plant Science* 342:112023
91. Li J, Pang Q, Yan X. 2023. Unique features of the m^{6}A methylome and its response to salt stress in the roots of sugar beet (*Beta vulgaris*). *International Journal of Molecular Sciences* 24:11659
92. Zhao Y, Guo Q, Cao S, Tian Y, Han K, et al. 2022. Genome-wide identification of the *AlkB* homologs gene family, *PagALKBH9B* and *PagALKBH10B* regulated salt stress response in *Populus*. *Frontiers in Plant Science* 13:994154
93. Hu J, Manduzio S, Kang H. 2019. Epitranscriptomic RNA methylation in plant development and abiotic stress responses. *Frontiers in Plant Science* 10:500
94. Luo W, Tang Y, Li S, Zhang L, Liu Y, et al. 2023. The m^{6}A reader SiYTH1 enhances drought tolerance by affecting the messenger RNA stability of genes related to stomatal closure and reactive oxygen species scavenging in *Setaria italica*. *Journal of Integrative Plant Biology* 65:2569–86
95. Wang Z, Tang K, Zhang D, Wan Y, Wen Y, et al. 2017. High-throughput m6A-seq reveals RNA m6A methylation patterns in the chloroplast and mitochondria transcriptomes of *Arabidopsis thaliana*. *PLoS One* 12:e0185612
96. Luo JH, Guo T, Wang M, Liu JH, Zheng LM, He Y. 2024. RNA m^{6}A modification facilitates DNA methylation during maize kernel development. *Plant Physiology* 194:2165–82
97. Liufu Y, Xi F, Wu L, Zhang Z, Wang H, et al. 2023. Inhibition of DNA and RNA methylation disturbs root development of moso bamboo. *Tree Physiology* 43:1653–74
98. Li J, Tian W, Chen T, Liu QY, Wu HW, et al. 2025. N^6-methyladenosine on the natural antisense transcript of NIA1 stabilizes its mRNA to boost NO biosynthesis and modulate stomatal movement. *Molecular Plant* 18:151–65
99. Li Y, Wang Y, Vera-Rodriguez M, Lindeman LC, Skuggen LE, et al. 2024. Single-cell m^{6}A mapping *in vivo* using picoMeRIP-seq. *Nature Biotechnology* 42:591–96
100. Hu L, Liu S, Peng Y, Ge R, Su R, et al. 2022. m^{6}A RNA modifications are measured at single-base resolution across the mammalian transcriptome. *Nature Biotechnology* 40:1210–19