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EPITRANSCRIPTOMICS IN FRUIT DEVELOPMENT AND STRESS RESPONSES: THE EMERGING ROLE OF RNA MODIFICATIONS

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ABSTRACT

In plant biology, the study of chemical changes on RNA transcripts, or epitranscriptomics, has become a crucial regulatory layer. There are more than 170 RNA modifications, and the most common one in mRNA is N^6-methyladenosine (m^6A). These changes function as dynamic "rheostats," adjusting gene expression in response to environmental stressors and developmental cues by modifying RNA splicing, stability, localization, and translation. Key RNA markers (m^6A, 5-methylcytosine [m^5C], pseudouridine, N^1-methyladenosine [m^1A], etc.) are now known to affect fruit growth, ripening, and quality in horticultural fruit crops. For instance, m^6A demethylation by SlALKBH2 speeds up ripening in tomatoes (a climacteric fruit) by upregulating the ripening DNA demethylase SlDML2. m^6A deposition on ABA biosynthesis/signaling transcripts (NCED5, AREB1, ABAR) in non-climacteric strawberries improves their stability and translation, which ABA-dependently promotes ripening. Further research relates RNA modification readers to fruit characteristics (for example, apple YTH readers influence disease resistance, whereas tomato YTH-domain proteins modify the translation of fragrance genes). Transcriptome-wide and tailored study of RNA marks is made possible by CRISPR/dCas13-based editing and emerging epitranscriptome-mapping technologies (MeRIP-seq, nanopore direct RNA sequencing, etc.). Finding out how RNA alterations affect color, taste, texture, and stress tolerance may be possible by combining epitranscriptomics with transcriptomics, proteomics, and metabolomics. RNA modifications (m^6A, m^5C, Ψ, m^1A) in important fruit crops (tomato, grape, banana, apple, mango, citrus, strawberry, etc.) are summarized in this review along with their molecular writers, erasers, and readers, as well as their functions in development, quality, and biotic/abiotic stress. In order to leverage epitranscriptomic control for better fruit crop production, we highlight developing technologies (such as m^6A-CLIP, nanopore sequencing, and CRISPR epitranscriptome editing) and talk about multi-omics techniques and breeding/biotech potential.

Keywords: Epitranscriptomic, Fruit Development, Stress Responses, RNA Modifications

Introduction

The transcriptional, post-transcriptional, translational, and post-translational levels all influence the expression of plant genes. Fruit growth and ripening have long been investigated in relation to epigenetic DNA and histone modifications, but "epitranscriptomics" chemical changes on RNA has just lately drawn interest. Without altering the sequence, these RNA marks which are inserted and erased by certain writers and erasers and identified by reader proteins can dynamically control the destiny of mRNA (Parker *et al*., 2021). Plants can quickly alter gene expression in response to changing circumstances because to the more than 170 RNA modifications that have been identified (Parker *et al*., 2021). The most notable of them is m^6A (N^6-methyladenosine), which forms a reversible mark on mRNA similarly to DNA 5-methylcytosine. Other examples include N^1-

methyladenosine (m^1A), 5-methylcytosine in RNA (m^5C), pseudouridine (Ψ, an isomer of uridine), and N^6,2′-O-dimethyladenosine (m^6A-m), which are all deposited by certain enzymes (writers) and eliminated by demethylases (erasers). These changes fine-tune gene expression by affecting mRNA splicing, stability, localization, and translation efficiency. It is becoming evident how important epitranscriptomic control is in plants. Pseudouridylation may change the identity of codons or ribosome interactions, and m^6A can label transcripts for stabilization or destruction based on context. These RNA modifications enable precise responses to stress and developmental cues. Stress-responsive transcripts experience a change in m^6A levels under heat or drought stress, which prioritizes stress genes and speeds up the degradation of non-critical mRNAs (Hu *et al*., 2021). Likewise, it has been shown that stress raises pseudouridine levels, which in turn increases the production of defense proteins (Sun *et al*., 2019). It is believed that dynamic regulation is quicker and more adaptable than transcriptional control alone. Accordingly, epitranscriptomic markers combine internal and external signals, functioning as "RNA epigenome" switches (Parker *et al*., 2021). Fruit crops with intricate developmental plans include tomatoes, grapes, bananas, apples, mangoes, citrus fruits, strawberries, and more. The two main categories of fruits are climacteric (tomato, banana, apple) and non-climacteric (ABA-influenced ripening; strawberry, grape, citrus) (Zhou *et al*., 2021). While abscisic acid (ABA) is a major factor in non-climacteric fruits, ethylene controls ripening (softening, color change, and taste) in climacteric fruits (Zhou *et al*., 2021). Hormone routes and transcriptional regulators in these systems have been extensively studied, but RNA alterations as regulators of fruit growth and quality have just lately come into our attention. According to preliminary research, m^6A dynamics coincide with important ripening events. For instance, the tomato's m^6A demethylase SlALKBH2 is necessary for regular ripening, connecting m^6A to ethylene signaling pathways (Zhou *et al*., 2019; Shen *et al*., 2024). The science of epitranscriptomics is developing quickly. m^6A sites have been mapped transcriptome-wide by high-throughput techniques (MeRIP-seq, miCLIP, DART-seq, etc.), and single-molecule detection of changes without amplification is now possible thanks to Nanopore direct RNA sequencing (Guo *et al*., 2022; Leger *et al*., 2021). In the meanwhile, alterations to certain RNAs may be targeted using CRISPR-based tools (e.g., dCas13 coupled to writer/eraser domains) (Shi *et al*., 2024). These discoveries might clarify the ways in which RNA markers affect fruit characteristics. With an emphasis on m^6A, m^5C, Ψ, and m^1A, this article offers a thorough summary of the state of knowledge about RNA changes in fruit crops. We talk about how the molecular machinery writers, erasers, and readers affects abiotic and biotic stress tolerance as well as fruit growth and ripening and quality (color, taste, and texture). Additionally, we discuss applications in breeding and biotechnology and highlight new methods for epitranscriptome engineering and analysis, such as multi-omics integration and epigenome editing.

The RNA Modification Landscape in Plants

Key modifications: Numerous internal mRNA changes are seen in plants. The most prevalent is N^6-methyladenosine (m^6A), which is found in consensus "RRACH" motifs and is enriched in hundreds of transcripts' 3′ UTRs and at stop codons (Guo *et al*., 2022; Zhou *et al*., 2021). N^1-methyladenosine (m^1A) (often at start codons/5′ UTRs), N^6,2′-O-dimethyladenosine (m^6A_m) at cap-adjacent sites, N^7-methylguanosine (m^7G) at the cap, N^4-acetylcytidine (ac^4C), and 5-methylcytosine (m^5C), whose writers include the NSUN family of methyltransferases, are other noteworthy mRNA modifications. Although they also exist in mRNAs, the modified nucleotides pseudouridine (Ψ) and 2′-O-methylation (Nm) are prevalent in rRNAs and tRNAs. According to a recent assessment, mapping difficulties have led to a lack of understanding of Ψ and Nm (among many others) in plants (Motorin & Helm, 2022). Together, these changes broaden the genetic code: m^6A may modify local RNA structure to affect splicing or translation (also known as the "m^6A switch"), and Ψ modifies base-pairing, perhaps recoding mRNA (Sun *et al*., 2019; Zhong *et al*., 2013). Readers, writers, and erasers: Arabidopsis is significantly responsible for the elucidation of the m^6A enzymatic mechanism in plants. MTA (homologous to METTL3), MTB (METTL14), FIP37 (WTAP), VIRILIZER (VIR), and HAKAI are examples of methyltransferase "writers" (Parker *et al*., 2021; Růžička *et al*., 2017). AlkB family proteins, such as ALKBH9B and ALKBH10B in Arabidopsis, are demethylases, or "erasers," that eliminate m^6A. YTH-domain proteins (also known as ECTs) are examples of "readers," which are proteins that bind m^6A-modified RNAs. Arabidopsis ECT2/3/4, for instance, are YTH readers that control growth. Orthologs of these have been found in fruit crops: apple and strawberry have their own sets (commonly referred to as YTH or YTP proteins), while tomato contains SlMTA, SlMTB, SlFIP37, SlALKBH2/3, and SlYTH1–9. Target RNAs may be stabilized or destabilized by readers. The ability of a YTH reader (MhYTP2) to bind and encourage the breakdown of transcripts of a powdery

mildew susceptibility gene (MdMLO19) in apples is noteworthy (Guo *et al*., 2022). It is NSUN methyltransferases that catalyze RNA m^5C. NSUN2 has been connected to stress reactions in Arabidopsis (Tang *et al*., 2020). H/ACA snoRNAs or PUS (pseudouridine synthase) enzymes install pseudouridine. Although rRNA and tRNA are the most well-known examples of pseudouridylation, new eukaryotic research have shown Ψ in mRNAs, which are often abundant in CDS or 3′-UTRs and impact translation and stability. The mapping of Ψ in plants is still in its infancy (Xie *et al*., 2022). The complex that writes m^1A is homologous to yeast TRMT6/61; its roles in plants are not well understood. Although research on plants is still in its infancy, other alterations (ac^4C, m^7G) exist and may affect translation efficiency and cap-binding.

Detection Technologies for RNA Modifications

RNA modification mapping and quantification methods are essential for comprehending epitranscriptomic control. The traditional method, known as MeRIP-seq (m^6A-seq), involves breaking up RNA, immunoprecipitating it with an anti-m^6A antibody, and then sequencing it to identify methylated areas at a resolution of around 100 nt (Guo *et al*., 2022). Crosslinking is added using improved techniques (miCLIP, m^6A-CLIP, and PA-m^6A-seq) to identify the precise changed nucleotide. C-to-U mutations are induced close to m^6A sites using the enzyme-based technique DART-seq, which fuses the deaminase APOBEC1 to a m^6A-binding domain (Meyer, 2019). Bisulfite sequencing (BS-seq) may detect methylated Cs for m^5C by converting unmodified C to U (Yang *et al*., 2019). In order to identify changes without the need of antibodies, chem-seq techniques and enzyme-based techniques (m^6A-REF-seq, MAZTER-seq) have recently surfaced (Xiao *et al*., 2023). Long-read direct RNA sequencing using nanopores is revolutionary because base-modification calling is made possible by changes to the ionic current signature that occur when an RNA strand moves through a nanopore (Leger *et al*., 2021). Plant epitranscriptomes have been effectively profiled using nanopore DRS; Arabidopsis mutants devoid of m^6A writers, for instance, exhibit distinct nanopore signals at m^6A locations (Leger *et al*., 2021). Although algorithms specific to plants are still being developed, this method can identify m^6A, m^5C, Ψ, etc., at the single-molecule level. Mass spectrometry (LC-MS/MS) is able to measure the global extent of RNA alterations. Epitranscriptomics will soon be able to map RNA markers with cellular precision thanks to single-cell and spatial transcriptomics.

New technologies in synthetic biology enable alteration of the epitranscriptome beyond detection. To install or delete m^6A at specific transcripts, the RNA-targeting Cas protein CRISPR/dCas13 may be coupled to writer or eraser domains (Shi *et al*., 2024). For example, a particular mRNA in plants may be methylated by a dCas13-METTL3 fusion and demethylated by a dCas13-ALKBH10B fusion. According to early research, plants can undergo targeted m^6A editing (Shi *et al*., 2024). These instruments provide accurate analysis of the role of RNA modification on specific genes and may one day be used to produce crops with customized epitranscriptomes. All things considered, the epitranscriptomics toolset presently consists of mass spectrometry, enzyme-based sequencing, nanopore long reads, antibody/immunoprecipitation techniques, and CRISPR-based editing (Guo *et al*., 2022; Shi *et al*., 2024).

m^6A and Fruit Development/Ripening

General observations

m^6A is dynamically controlled throughout development and ripening, according to studies conducted in model fruit systems. As the fruit ripens, m^6A levels on several mRNAs in tomatoes, a traditional climacteric fruit, drop (Zhou *et al*., 2019). This worldwide decrease is comparable to the ripening-related drop in DNA methylation. The trend in non-climacteric strawberries is different: during the commencement of ripening, m^6A deposition rises on certain genes (Zhou *et al*., 2021). The different hormonal regulation (ethylene vs. ABA) in climacteric vs non-climacteric fruits are probably the cause of these variations (Zhou *et al*., 2021). m^6A patterns seem to be adapted to each fruit type's developmental program. The ethylene-insensitive mutant Neverripe (Nr) in tomatoes, for instance, exhibits higher m^6A levels on several transcripts compared to the wild-type, indicating that ethylene signaling often inhibits m^6A on ripening genes (Zhou *et al*., 2019). m^6A is also involved in the development of embryos and seeds: Arabidopsis mutants that lack the m^6A writer MTA are harmful to embryos, and m^6A mutants exhibit abnormalities in the creation of leaves and flowers (Shen *et al*., 2016). Targeted mutations have been instructive in fruits. Tomato ripening is significantly delayed when the m^6A eraser SlALKBH2 is CRISPR knocked out (Shen *et al*., 2024). SlALKBH2 demethylates the transcript of SlDML2, a DNA demethylase necessary for ripening, according to molecular studies. The fruit is locked in an unripe condition when SlALKBH2 is lost because it increases m^6A on SlDML2 mRNA, decreasing its stability (Shen

et al., 2024; Zhou *et al*., 2019). This creates a mechanistic connection: fruit ripening is regulated by the integration of the epigenome (DNA methylation) and the epitranscriptome (m^6A on mRNA) (Shen *et al*., 2024). Similar cross-talk is seen in Arabidopsis, where m^6A methylation has been shown to affect histone and chromatin states, indicating shared regulatory loops (Zhong *et al*., 2013; Cai *et al*., 2023).

Tomato (*Solanum lycopersicum*)

One of the most popular models for plant epitranscriptomics is the tomato. Zhou *et al*. (2019) found hundreds of transcripts with stage-specific m^6A peaks and produced the first fruit m^6A methylome in a tomato. They discovered that the hypermethylated Colorless non-ripening (Cnr) mutant also has elevated m^6A across around 1100 transcripts, which is in line with whole-fruit tests (Zhou *et al*., 2019). In wild-type tomatoes, m^6A methylation often decreased as the tomato ripened. SlALKBH2 controlled the balance by removing m^6A from SlDML2 mRNA, which ensures high amounts of SlDML2 to promote DNA ripening and demethylation. SlALKBH2's function was validated by CRISPR knockout: SlALKBH2 deletion increased m^6A on the SlDML2 transcript, reduced its quantity, and postponed ripening by around three to five days (Shen *et al*., 2024).

In addition to SlDML2, m^6A also affects tomato genes that regulate fruit size and growth. Using methyltransferase/demethylase inhibitors, Hu *et al*. (2022) demonstrated that ripening was retarded by blocking demethylases (with MA treatment) and hastened by lowering m^6A (with methyltransferase inhibitor DZNep) (Hu *et al*., 2022). Additionally, 24 tomato genes implicated in the m^6A machinery (writers, erasers, and readers) were discovered by Yin *et al*. (2022). Dwarf plants with delayed fruit ripening were produced by virus-induced silencing of SlMTA/MTB or YTH-domain readers (SlYTH1, SlYTH3, SlYTH7), demonstrating the need of these genes for healthy development (Yin *et al*., 2022). Therefore, m^6A recognition and methylation are essential for tomato fruit development and vegetative growth. It's interesting to note that SlYTH2, a YTH-domain reader, has two functions: in addition to influencing when ripening occurs, a recent PNAS research revealed that SlYTH2 deletion enhances the synthesis of fragrance (Bian *et al*., 2024). SlYTH2 typically binds to the mRNAs of aroma-synthesis enzymes (carotenoid cleavage dioxygenase CCD1B and hydroperoxide lyase HPL) in a m^6A-dependent way. It suppresses the translation of certain fragrance mRNAs and forms liquid-like condensates with translation factors (Bian *et al*., 2024). This inhibition is lifted when SlYTH2 is lost, increasing volatile synthesis. This is an example of how a m^6A reader may modify mRNA translation to fine-tune fruit quality attributes (in this case, taste compounds) (Bian *et al*., 2024).

Measurements of other RNA changes in tomatoes have been made. During ripening, Guo *et al*. (2022) analyzed m^1A, m^5C, and ac^4C in both the Nr mutant and wild-type Ailsa Craig (Ma *et al*., 2024a). They discovered that whereas m^5C levels rise during ripening, m^1A and ac^4C levels decrease. Additionally, ethylene-insensitive Nr mutant fruits are not like the natural type: According to Ma *et al*. (2024a), Nr fruits exhibit reduced m^1A and changed ac^4C alterations, indicating that ethylene signaling affects RNA modifications. Though their dynamic tendencies suggest different regulatory functions (e.g., potentially m^5C accumulation favors certain ripening processes), the biological relevance of these markers in tomatoes is still unclear. In conclusion, research on tomatoes shows that RNA methylation networks which include writers, erasers, and readers are essential for fruit growth, ripening pace, and quality characteristics including fragrance.

Strawberry (*Fragaria* spp.)

ABA, not ethylene, drives the ripening of strawberries, which are non-climacteric fruits. Transcriptome-wide m^6A mapping was carried out by Zhou *et al*. (2021) in diploid strawberries (Fragaria vesca) throughout the ripening phases (Zhou *et al*., 2021). During the commencement of ripening, they discovered a significant displacement of m^6A. Like many plants, m^6A peaks were concentrated near stop codons and 3′-UTRs in early fruit (growth stage S6) (Zhou *et al*., 2021). But when ripening began (stage RS1), stop-codon/3′-UTR peaks decreased and the proportion of m^6A in coding sequences (CDS) increased (Zhou *et al*., 2021; Yang *et al*., 2019). This change indicates that mature fruit has more m^6A marks in its 5′ coding regions. Remarkably, genes with m^6A in 3′-UTRs were downregulated, whereas those with m^6A in the CDS tended to have higher mRNA abundance (Yang *et al*., 2019; Liu *et al*., 2015). The former group included important genes in the ABA biosynthesis/signaling pathway (NCED5, ABAR, and AREB1), which were markedly elevated during ripening and gained m^6A in their CDS (Zhou *et al*., 2021). Strawberry methyltransferases MTA/MTB are necessary for ripening, as shown by Zhou *et al*.; inhibiting them prevented normal color and softening. Accordingly, m^6A drives the non-climacteric ripening pathway in strawberries by acting via ABA-related genes (Zhou *et al*., 2021). Tang *et al*. (2024) found a

complementary mechanism in the octoploid strawberry (Fragaria × ananassa). The m^6A demethylase ALKBH10B was shown to be a positive ripening regulator. ALKBH10B is expressed in response to ABA signaling (via ABF3), and it stabilizes SEP3 mRNA by removing m^6A from its 3′-UTR (Tang *et al*., 2024). A MADS-box transcription factor called SEP3 promotes the growth of ripening genes. Thus, high SEP3 levels are guaranteed by ALKBH10B-mediated demethylation, which further initiates ripening. The tomato and strawberry examples together demonstrate that timely fruit ripening depends on preserving appropriate m^6A homeostasis on important transcripts (hormone pathway genes, transcription factors). The process may be derailed if either writers or erasers are disrupted (Tang *et al*., 2024).

Kiwifruit and others

Similar similarities are suggested by emerging evidence in other fruits. Su *et al*. (2024) mapped m^6A throughout ripening in kiwifruit (Actinidia) and discovered that total m^6A levels decrease as fruit ages. Ripening-related genes are the primary targets of the m^6A demethylase AcALKBH10. AcALKBH10 loss causes increased m^6A on genes involved in sugar and acid metabolism, changing their expression and postponing the buildup of sugars and organic acids that are essential for ripening (Su *et al*., 2024). This suggests that metabolites essential to fruit quality are once again modulated by m^6A. Direct profiling under stress has shown m^6A alterations in apples (see below). Less research has been done on other fruit crops; there are currently no particular findings on m^6A in the ripening of citrus, bananas, mangos, or grapes. However, it is probable that similar epitranscriptomic systems function in plants because to the conserved existence of m^6A machinery.

Epitranscriptomics and Fruit Quality Traits

Fruit quality encompasses color, flavor/aroma, texture, and nutrient content. RNA modifications have been linked to these traits primarily via regulation of relevant biosynthetic genes.

- **Flavor and aroma:** Fatty acids (via HPL) and carotenoids (through CCD enzymes) are the sources of volatile chemicals in tomatoes. As mentioned, m^6A-marked HPL and CCD1B transcripts are bound by the YTH-domain reader SlYTH2 to suppress their translation (Bian *et al*., 2024). These genes are derepressed when SlYTH2 is lost, which increases the synthesis of volatiles and, therefore, the strength of scent (Bian *et al*., 2024). One of the first clear instances of an epitranscriptomic regulator influencing a dietary characteristic is this one. It implies that taste profiles might be altered by adjusting RNA readers or the m^6A status of certain transcripts. Through SEP3, the ABA-related process in strawberries indirectly influences the color of the anthocyanins and the acid/sugar balance. Although its biological influence on fruit color is still being defined, another research shown that the m^6A reader FvECT2 binds mRNAs in the anthocyanin pathway (e.g., FvCHI, FvDFR) to control color accumulation.
- **Texture (softening):** Cell-wall enzymes such as expansins, pectin methylesterases, and polygalacturonases are involved in the softening of fruit. m^6A on cell-wall genes in fruits has not yet been identified by direct epitranscriptomic analysis. Nonetheless, it is conceivable that the transcription of softening enzymes is indirectly impacted by m^6A or other marks on ripening regulators (such as SEP3). Such connections may be discovered in future research using MeRIP-seq in fruit at various firmness stages.
- **Color and nutrition:** Epitranscriptomics probably affects pigment pathways in addition to the FvECT2 story mentioned above. For instance, it has been shown that m^6A controls the pigmentation genes in Arabidopsis, a non-fruit plant. The production of carotenoid or anthocyanin may be impacted by m^6A if fruit has comparable regulatory circuits. Although there are currently no direct citations, the framework suggests that authors or readers may alter any important mRNA (transcription factor or enzyme) in these pathways. There is still much to learn since this study is still in its infancy.
- **Metabolites of nutrients:** Epitranscriptomics may regulate sugars, acids, and vitamins via upstream genes. AcALKBH10 influences the buildup of sugar and acid in kiwifruit (Su *et al*., 2024). Recent research employing nanopore sequencing in apples discovered that a decrease in m^6A and a weakened fungal defense (Alternaria resistance) are caused by changes in sorbitol metabolism, a main apple sugar. It suggests that RNA methylation and sugar-signaling interact to affect fruit health, although it hasn't been peer-reviewed yet. In conclusion, preliminary data indicates that m^6A regulators may influence fruit quality via regulating metabolic genes and hormone transmission. We anticipate finding a lot more RNA targets in taste, color, and texture pathways as mapping technologies advance.

RNA Modifications in Stress Tolerance

Fruit crops face myriad stresses. Epitranscriptomic marks enable rapid stress-responsive gene regulation, and evidence is accumulating for roles in both abiotic and biotic tolerance.

Abiotic stress (drought, heat, cold, salinity)

Environmental stress causes changes in m^6A and other markers, according to global assessments across plants. For example, m^6A on stress-related transcripts is usually redistributed in response to heat or drought (Hu *et al*., 2021). According to research, heat stress induces m^6A to preferentially preserve or translate stress-response mRNAs while destabilizing non-essential mRNAs (shunting them to decay) in Arabidopsis, rice, and other plants (Hu *et al*., 2021; Wang *et al*., 2022b). In particular, m^6A marks on transcription factors and heat-shock protein (HSP) transcripts speed up their translation in response to heat or drought, whereas m^6A marks on other transcripts speed up their degradation (Hu *et al*., 2021; Wang *et al*., 2022b). Plants benefit from this reprogramming by having their resources redirected toward stress resistance. Additionally, m^5C is susceptible to stress; for instance, heat stress raises m^5C in rice chloroplast RNAs, which impacts the generation of ROS (Tang *et al*., 2020). Under stress, pseudouridine levels increase, which encourages the synthesis of defense proteins (Sun *et al*., 2019).

Concrete examples are still being developed in fruit crops. Heat-smudge in tomatoes is one example of the quality loss that may result from drought and high temperatures during fruit growth. Coordinated alterations in the transcriptome, proteome, and m^6A methylome were seen in a multi-omics study of tomatoes under cold stress, indicating that transcriptional adaptations to cold are driven by m^6A reprogramming. In water-stressed tomato fruit under drought, RNA-seq revealed that exogenous ABA, a drought signal, modifies m^6A patterns on stress transcripts and revealed differential expression of several epitranscriptome enzyme genes (e.g., SlMTA/MTB increased). The basic concept suggests that m^6A may regulate ABA production and signaling transcripts to shut stomata in water shortage, as shown in Arabidopsis drought response, even if the specific processes in fruit per se are not entirely understood (Hu *et al*., 2021). Similarly, research on plants under salt stress suggests that m^6A alterations influence ion transporter expression; this theory has to be confirmed for each fruit.

Biotic stress (pathogens, pests)

Plant-pathogen interactions also include epitranscriptomic control. According to recent studies, m^6A may affect susceptibility, and plant viruses and bacteria can alter host m^6A machinery (Martinez-Perez *et al*., 2017). For instance, Arabidopsis mutants with m^6A methylation defects shown enhanced resistance to certain bacterial and fungal diseases, maybe as a result of altered expression of defense genes (Martinez-Perez *et al*., 2017). There are developing special instances in fruit crops. Malus halliana's YTH-domain reader MhYTP2 was overexpressed in apples, increasing their resistance to powdery mildew (Guo *et al*., 2022). Two MLO genes (MdMLO19 and MdMLO19-X1) that are susceptibility factors for powdery mildew have their mRNAs bound and destabilized by MhYTP2. At the same time, overexpression of MhYTP2 improved the translation efficiency of many transcripts of antioxidant enzymes. Accordingly, it has been shown that an epitranscriptomic reader may both increase the production of defense genes and decrease susceptibility genes (Guo *et al*., 2022). This suggests that host defense may be reprogrammed by altering readers. Additionally, the research discovered that MhYTP2 overexpression increased total m^6A levels, indicating a feedback loop between methylation and binding.

Furthermore, an unreviewed work that used nanopore direct RNA sequencing on apples found that a major loss of m^6A on transcripts and a corresponding vulnerability to the fungal infection Alternaria alternata resulted from a decrease in sorbitol production, a sugar that is essential for apples. This suggests a defensive relationship between m^6A and metabolic status (sugar signals). It highlights the links between epitranscriptomics and biotic stress, however specifics are still under peer review. Although less is known about other fruits, we anticipate that m^6A will play a part in fungal resistance and viral defense (as shown by research on rice viruses). For example, it is worthwhile to look at how the Solanum YTH proteins (Tomato YTH1/2) may affect a person's vulnerability to Botrytis or Phytophthora. Lastly, pseudouridine may also play a role. Although there is a dearth of plant data, stress studies indicate that Ψ generation is enhanced during defense, perhaps via stress-activated pseudouridine synthases (Sun *et al*., 2019). In conclusion, RNA changes are attractive targets for improving disease resistance in fruit crops because they alter plant immune networks.

RNA Modification Machinery in Fruit Crops

Writer and erasers:

Fruit species seem to have the majority of plant m^6A writers preserved. Homologs of MTA, MTB, FIP37, VIR, HAKAI, and HIZ2 (KIAA1429 homolog)

have been found in tomato, apple, grape, strawberry, and other plants by genomic analysis. Although there are few functional investigations, expression data show that MTA/MTB transcripts often surge during fruit ripening or expansion. FvMTA/FvMTB expression, for instance, increases in strawberries when ripening begins (Zhou *et al*., 2021). Strawberry ripening is delayed when MTA or MTB are knocked down (via VIGS), underscoring the importance of these genes (Zhou *et al*., 2021). In a similar vein, tomato SlMTA/MTB knockdown results in delayed fruiting and dwarfism (Yin *et al*., 2022). Fruits on the eraser side include members of the ALKBH5/9/10 family. SlALKBH2 and SlALKBH3 are found in tomatoes; during ripening, SlALKBH2 demethylates SlDML2 mRNA (Zhou *et al*., 2019). Interestingly, strawberry FvALKBH10B demethylates SEP3 mRNA to promote ripening, whereas Arabidopsis's ALKBH10B demethylates regulators of leaf and root development (Tang *et al*., 2024). AcALKBH10 targets ripening genes in kiwifruit (Su *et al*., 2024). These results highlight the frequent action of demethylases on certain developmental transcripts. The targets of each eraser are starting to be identified by genetic research (CRISPR KO, RNAi). Redox control of demethylases is suggested by emerging data. In tomatoes, oxidative circumstances (H_2O_2 buildup) cause inactive ALKBH2 homodimers to develop, stabilizing SlALKBH2 and speeding up ripening (Zhou *et al*., 2019). In contrast, ALKBH2 may be reduced to monomers by the thioredoxin NTRC, which slows down the rate of ripening (Zhou *et al*., 2019). Thus, metabolism and the epitranscriptome are linked, with the cellular redox state influencing the eraser's own activity. It is uncertain whether other fruits have comparable redox control, but it is an intriguing prospect for further research.

For further changes: In fruit, m^5C writers (NSUN family) and erasers (perhaps TET-like oxidases for RNA) are mostly unknown. Fruit-specific information is lacking, despite the abundance of pseudouridine synthases (PUS). Site-specific Ψ formation on mRNAs is dynamic in mammals, but it is just now becoming apparent in plants. The conservation of some plant PUS enzymes points to potential functions in development or stress. Although the genomes of plants include m^1A writers (TRMT61A homologs), fruit contexts have not yet been investigated.

Readers: Proteins with a YTH domain act as m^6A readers. There are two clades of plants: YTHDC/YTHDF-like and ECT (plant-specific). Eight YTH proteins (SlYTH1–8) are found in tomatoes (Yin *et al*., 2022). Functional experiments reveal a variety of roles: in addition to SlYTH2 (see above), development was delayed by SlYTH1, SlYTH3, and SlYTH7 knockdowns (Yin *et al*., 2022). ECT2/3/4 binds m^6A in Arabidopsis to regulate organogenesis. Although particular strawberry readers have not been identified, it is possible that an ECT homolog will bind the ABA-pathway transcripts in strawberries. Defense and stress gene transcripts are bound by the YTH-domain protein MhYTP2 in apples (Guo *et al*., 2022). It seems that plant YTH readers have the ability to either stabilize or destabilize targets. For example, MhYTP2 binding in apples caused MdMLO19's mRNA to degrade (Guo *et al*., 2022), yet in other instances, Arabidopsis ECTs stabilize targets. The result is probably determined by the context (which gene, where m^6A is situated).

There are other readers: plants have ALY homologs, but it's unknown how specific their RNA is; animals' ALY proteins bind m^5C and affect export/translation. There are no known specialized reader proteins for pseudouridine. For m^6A, the YTH family is thus essential to a large portion of plant epitranscriptomic decoding. It is still unclear how to characterize fruit-specific readers, such as homologs of apples and pomegranates. Circuits are created by the interaction of writers, erasers, and readers; for example, ALKBH erasers rely on YTH proteins to decipher the altered code. Fruit models are gradually revealing this mechanism, but further research (protein-binding tests, knockout phenotypes) is still required.

Integration with Multi-Omics and Crop Improvement

The epitranscriptome interacts with other levels rather than functioning independently. It has been shown to be effective to combine m^6A maps with proteome and transcriptome (RNA-seq) data. For instance, Zhou *et al*. correlated m^6A variations with mRNA abundance in strawberries by integrating m^6A-seq and mRNA-seq (Zhou *et al*., 2021). By combining m^6A-seq, RNA-seq, and volatile profiling in tomatoes, for example, one may relate SlYTH2-mediated m^6A modifications to particular fragrance volatiles. Multi-omics techniques can also link epitranscriptomic changes to metabolite phenotypes. In one recent multi-omics investigation, tomato plants were exposed to cold stress and the m^6A methylome, proteome, and transcriptome were all examined at the same time. Co-regulated modules were discovered; certain mRNAs displayed cold-induced m^6A enrichment and associated protein accumulation, shedding light on the function of m^6A in cold adaption. These discoveries may be used in biotechnology and breeding. Differences in fruit

traits may be due to natural variation in RNA modification genes (or their target motifs). For example, variations in SlALKBH2 or its regulatory components may affect the shelf life of tomatoes. Epitranscriptome regulators may be targeted by marker-assisted selection or genome editing (CRISPR/Cas9); the CRISPR KO of SlALKBH2 mentioned above is an example of how altering an epitranscriptomic enzyme might change a phenotype (Shen *et al*., 2024). More specifically, it may be possible to modify certain m^6A sites in candidate genes using trans-acting RNAs or CRISPR-base editing (although this is yet speculative). One potential use of CRISPR/dCas13-based epitranscriptomic editing is the ability to up- or down-regulate particular transcripts during fruit ripening (e.g., fusing dCas13 to METTL3 or ALKBH10) (Shi *et al*., 2024). Using m^6A profiles, "epiGWAS" might investigate relationships between phenotypic and natural epitranscriptome variation for breeding purposes.

Furthermore, a comprehensive understanding of fruit regulatory networks may be created by integrating epitranscriptomics with DNA epigenetics (methylome) and small RNA profiling. Traditional and molecular breeding will ultimately benefit from an understanding of RNA modifications. For instance, choosing alleles that maintain favorable m^6A patterns under heat stress may result in heat-tolerant tomatoes; modifying m^6A on flavor genes may result in tomatoes with improved aroma; and adjusting readers may increase disease resistance or shelf life (Shen *et al*., 2024).

Emerging Tools and Future Directions

Techniques for researching RNA alterations have increased dramatically in recent years. In addition to those previously discussed, new techniques such as BID-seq (bisulfite-based for m^5C) and GLORI (chemical labeling for single-base m^6A detection) have shown nucleotide resolution in mammals (Shen *et al*., 2024); it is a top goal to apply these techniques to plants. Future developments in spatial and single-cell epitranscriptomics include the mapping of the epitranscriptome in certain fruit tissues (such as skin vs flesh) or cell types (such as vascular versus mesocarp) using technologies like MERFISH or Slide-seq tailored to RNA alterations (Lv *et al*., 2024). Cell-specific regulatory responsibilities, such as how m^6A in peel cells controls color development, might be revealed by such data. Additionally, CRISPR technology is developing. Precision epitranscriptome engineering is made possible by the discovery that dCas13 fusion proteins may add or delete m^6A on certain transcripts (Shi *et al*., 2024). This might be used with inducible systems (chemical or light-control) in future research to modify RNA markers over time. Additionally, designer RNA circuits might be made via synthetic biology. For instance, plants could be engineered to include a m^6A-responsive RNA element that only regulates transgene translation under stress. This calls an in-depth understanding of effector domains and recognition motifs, which are now the subject of intensive study. There are still a lot of gaps despite progress. As said, the majority of research has been on m^6A; m^5C, Ψ, and m^1A play mostly unknown functions in fruit. Profiling these markings in fruits will be made easier with the development of antibody-independent mapping (such as nanopore). We probably underestimate the variety of plant RNA modification readers since, for example, no plant homologs of the animal YTHDC1 (nuclear reader) have been described. Establishing causal linkages is a major difficulty in agricultural applications. Transgenerational impacts are complicated because epitranscriptomic changes do not change the genome way DNA edits do. However, heritable traits may result from mutations in writers/erasers (such as SlALKBH2). The idea of natural epigenetic variation, or RNA "epi-alleles," is fascinating: alleles that affect writer binding or RNA structure may be chosen. It would be beneficial to work with other countries to map the epitranscriptomes of various fruit kinds and connect them with characteristics.

Conclusion

One new area of fruit biology is epitranscriptomic alterations. The impact of RNA methylation, particularly m^6A, and associated markers on fruit growth, quality, and stress responses has been emphasized in this study. It has been shown that m^6A controls important regulatory genes in model fruit crops like tomatoes and strawberries, connecting RNA chemistry to hormone signaling and developmental circuits. The influence of these markings on mRNA destiny is mediated by novel reader proteins, which effect characteristics ranging from scent generation to ripening time. The area is advancing thanks to technologies like CRISPR/dCas13 editing, nanopore direct RNA-seq, and immunoprecipitation sequencing, which make it possible to study RNA changes both broadly and specifically throughout the transcriptome. In actuality, combining phenotyping, genomics, and epitranscriptomic information may lead to new fruit crop development opportunities. For instance, without altering coding sequences, RNA modification enzymes or reader interactions may be altered to improve taste or stress tolerance. To fully realize this promise, however, further study is needed to map the whole array of alterations in each fruit species, comprehend

the enzymatic networks (many of which are still unknown), and correlate certain RNA marks with particular phenotypes. We expect a comprehensive picture of "who writes, reads, and erases" each RNA mark in each fruit tissue as single-cell and multi-omics techniques advance. In the end, epitranscriptomics broadens our knowledge of fruit biology in an intriguing way. Examining RNA as a chemically active molecule allows us to understand a new level of regulation that controls how fruits grow, mature, and handle stress. To convert these discoveries into useful applications in molecular horticulture and sustainable agriculture, further multidisciplinary research will be necessary.

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