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Tomato fruit: Origin and its developmental regulation

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Abstract

Fruit development and ripening genes have a close relationship with the regulatory elements that control the development of floral organs. Furthermore, like with many other aspects of plant development, understanding the processes that drive fruit development and ripening necessitates disclosing both the genetic and epigenetic architecture that underpins gene structure and expression. Moreover, there is increasing evidence that epigenetic regulators are important in fruit development and ripening, and that they may work together with hormones and transcription factors. To determine particular chromatin states, epigenetic changes like-as DNA methylation, histone post-translational modifications, and noncoding RNAs can interact with one another. Developments in the plant's molecular biology have enabled researchers to surpass the limits of classical methodology of study for other crops especially the tomato's ancestor. In this review, we cover a variety of subjects, including the history of the tomato, the evolution of fruit ripening regulation, and the mechanisms relating to epigenetic regulation in tomato fruit ripening. These findings, according to researchers, may have a significant impact on crop development strategies in fruit-bearing species.

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1. INTRODUCTION

The tomato is a member of the Solanaceae family, which contains over 3,000 species, including many economically significant plants such as potatoes, eggplants, petunias, tobacco, peppers, and physalis (Barboza et al., 2016). Solanum is the largest genus within the Solanaceae family, containing between 1,250 and 1,700 species. Solanum species are found on all temperate and tropical continents, and their morphological and ecological diversity is remarkable. One of the characteristics that can be used as key identification for plants under the Solanaceae family is that they are known as herbs, shrubs or small trees (Moyetta et al., 2013). Besides that, its fruits are usually in capsule form or berry-like with numerous flattened seeds. Most of the Solanaceae family members have actinomorphic or zygomorphic and bisexual inflorescence but rarely do they appear to be unisexual. Solanum is likely the most economically significant genus, with crop species and numerous other species producing toxic or medicinal compounds (Alajmi et al., 2018).

Fruit, in terms of its botanical definition is a mature and ripened ovary of a flower. Flowering plants have the ability to produce seeds within an ovary or carpel, which is why they are also known as angiosperms (Greek angio, vessel + sperm, seed). Thus, fruits are confined to the angiosperms that represent nearly 90% of all extant plant species and dominate all the major terrestrial zones of vegetation (Condamine et al., 2020). Fleshy fruits can be divided into two subclasses which are climacteric fruits such as tomato and banana fruits that require a burst of respiration and ethylene production for ripening to occur and non-climacteric fruits that do not require a burst of respiration and ethylene production for ripening to occur such as strawberry and sweet orange fruits (Seymour et al., 2013b).

Genes influencing fruit development and ripening are closely connected to regulatory factors involved in modulating the development of floral organs, which is somewhat unsurprising given the discoveries in the last two decades (Seymour et al., 2013a). Furthermore, like with many other aspects of plant development, understanding the processes that drive fruit development and ripening necessitates disclosing both the genetic and epigenetic architecture that underpins gene structure and expression. Moreover, there is increasing evidence that epigenetic regulators are important in fruit development and ripening, and that they may work together with hormones and

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transcription factors (Anwar et al., 2021). Basically, epigenetic modifications are defined as mitotically or meiotically heritable changes in the genome activity which are not caused by the changing of genomic DNA sequence. Epigenetic modifications including DNA methylation, histone post-translational modifications (histone acetylation and methylation), histone variations and noncoding RNAs that can interact with each other to determine specific chromatin states, thereby activating or suppressing the gene expression (Tang et al., 2020).

This review will focus on the origin of the tomato, the development of regulation in ripening fruits and its epigenetic mechanisms. Discoveries on the role of epigenetics on plant development, especially fruit, might have a considerable impact on crop development tactics in fruit-bearing species.

2. ORIGIN OF TOMATO

The exact origins of tomato domestication are still unknown. Although there has been much discussion about the Peruvian and Mexican ideas, further research is still being done to determine their viability. The cultivated tomato *(Solanum lycopersicum L.*) (SL) belongs to the Solanaceae family and the *Solanum L. genus.* Its relatives in the wild are indigenous to western South America and the Galapagos Islands (Pailles et al., 2020). The closest wild ancestor of the tomato is *S. pimpinellifolium L.* (SP) which are found along the Peruvian and Ecuadorian coasts and are split into three primary genetic groupings that correlate to environmental variations (Figure 1) (Takei et al., 2021). There are two botanical varieties of *S. lycopersicum: S.l. var. Cerasiforme* and *S.l. var. lycopersicum* (SLL). *Solanum lycopersicum var cerasiforme* (SLC) is native to the Andean area of Ecuador and Peru, although it may also be found in subtropical climates across the world (Barboza et al., 2016). As a true wild species, SLC can be found in home gardens, along roads, in sympatry with tomato landraces, or as a cultivated crop. SLC also thrives in the humid habitats of Ecuador and Peru along the Amazon basin's eastern edge, whereas SP prefers the drier Peruvian beaches and valleys. Although there is no reproductive barrier between SP and SLC, the Andes mountains present formidable physical and ecological barriers to crossbreeding between these species (Bergougnoux, 2014).

Recent research based on the analysis of SNPs not only confirms that *S. lycopersicum var. cerasiforme* is not the ancestor of the cultivated tomato, but it also strengthens the model that pre-domestication of the tomato occurred in the Andean region (Peruvian hypothesis), with domestication being completed in Mesoamerica (Mexican hypothesis), followed by its introduction to Europe by the Spaniards in the 16th century, and spread worldwide (Li et al., 2022). The final identification of tomatoes stated the normal cultivated tomato as *S. lycopersicum* along with its other twelve wild relatives (Bergougnoux, 2014).

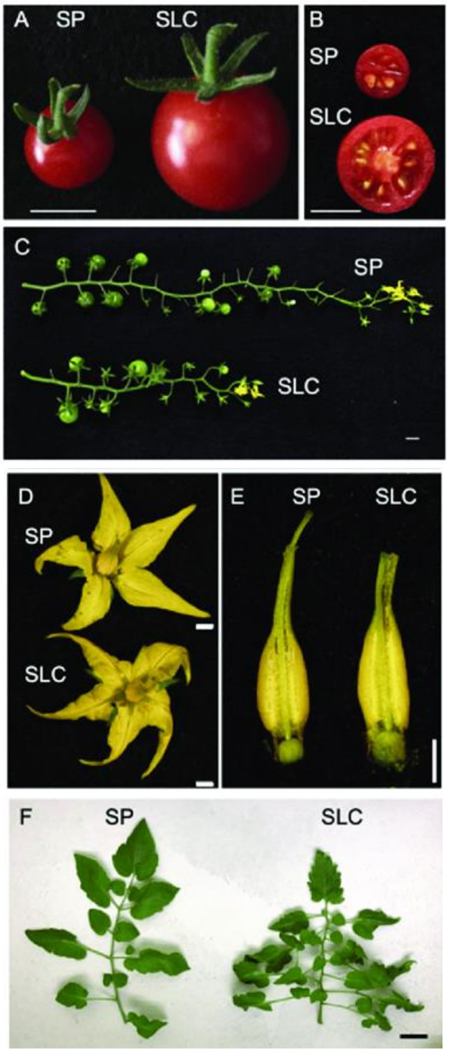

Figure 1: Morphology of *S. pimpinellifolium* (SP), possible ancestor of modern cultivated tomato compared to modern tomato *Solanum lycopersicum L.* (SLC) taken from (Takei et al., 2021).

3. CYTOGENETIC OF TOMATO

Tomato (*Solanum lycopersicum* L.) is considered as one of the economically important crops under family Solanaceae. This species has a diploid genome which consists of chromosome number 2n=2x=24. It is also referred as a model plant species due to its diploid, compact, relatively sequenced genome and its large genetic and genomic resources (Ranjan et al., 2012). A previous study found that there are 24 and 26 chromosomes in different cultivated tomato varieties that might be caused by thermodynamic effects (Fedorova, 1969; Hemantaranjan, 2014). Chromosome number and structure variation as well as genome size information play an important role in the study of species relationships among closely related plants and the genetic diversity of species (Gianfranco et al., 2008; Midin et al., 2018; Tlili et al., 2020). The tomato originated in South America and was first domesticated in Mexico. Its domestication history has been thought to consist of two major transitions in Latin America: (1) one from wild *Solanum pimpinellifolium* L. to a semidomesticated intermediate, *S. lycopersicum* L. var. cerasiforme in South America; and (2) a transition from *S. lycopersicum* L. var. cerasiforme to fully domesticated *S. lycopersicum* L. var. *lycopersicum* in Mesoamerica (Razifard et al., 2020).

4. ECONOMIC IMPORTANCE OF TOMATO

Nowadays, tomatoes are one of the most consumed crops in many different countries including America, Australia, Europe, Africa and almost all around the globe. However, this is not always the case. Before they were cultivated widely, they were thought to have toxins and poisonous to the people who consumed them (Barboza et al., 2016). Several culinary historians declared that Americans did not consume tomatoes until the 19th century and apparently, the tomatoes were cooked for three hours to remove the alleged toxins. They were also once labelled as "Love apples" as the Colonial Americans claimed that tomatoes have aphrodisiac properties. Some agricultural historians also indicated that tomatoes were not recognized as field crops before the Civil War and a few decades after. Nevertheless, these myths were not scientifically proven due to unpublished manuscripts and unrecorded data prior to the Civil War era (Smith, 2013). Despite the various myths surrounding this crop species, new base knowledge and a new outlook on tomatoes boost its reputation until they were known and can be found worldwide (Bergougnoux, 2014).

From the economic perspective, tomatoes are not only sold fresh, but also as paste, soup, juice, sauce, powder, concentrate, and whole tomatoes. Tomatoes are one of the most widely consumed vegetables in the world, second only to potatoes and ahead of onions, and are likely the most popular garden crop (Figure 2). In 2011, global tomato production reached nearly 160 million tonnes, making it the seventh most important crop species, following corn, rice, wheat, potatoes, soy, and cassava (FAO, 2017). During the past two decades, tomato production and cultivation area have increased by twofold. Europe and the Americas were the most important producers 20 years ago, but today Asia dominates the tomato market, with China ranking first, followed by India, the United States, Turkey, Egypt, Iran, Italy, Brazil, Spain, and Uzbekistan (Costa & Heuvelink, 2018).

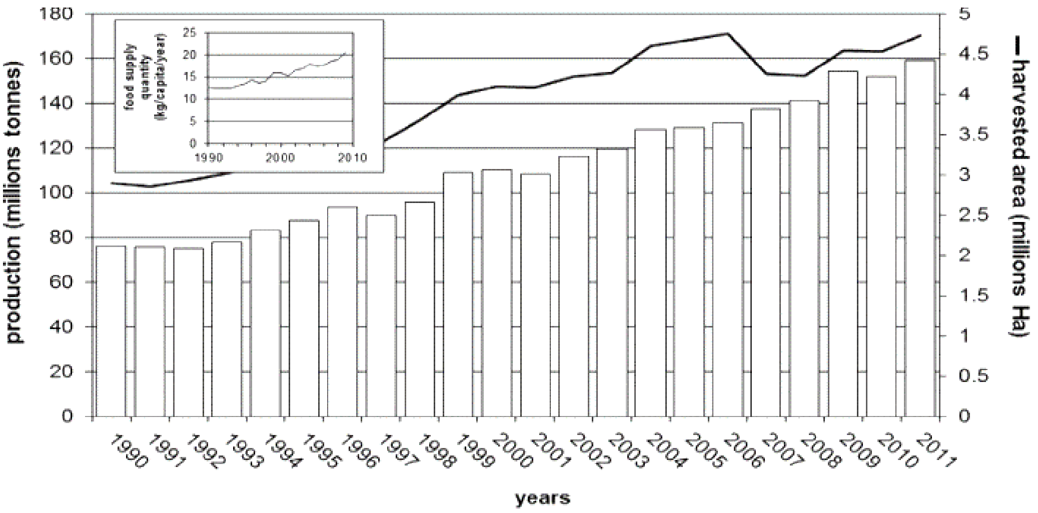

Figure 2: Total tomato production globally (Bergougnoux, 2014).

5. DEVELOPMENTAL REGULATION OF FRUIT RIPENING IN TOMATO

Fruit ripening is a complex developmental process that occurs at the same time as seed maturation. Thousands of genes influence the increasing softening or lignification of pericarp layers, the accumulation of sugars, acids, pigments, and the release of volatiles during the ripening process (Seymour et al., 2008). A better knowledge of the processes that cause fruit to ripe is essential for crop improvement. Mutations blocking the transition to ripe fruits in tomatoes have revealed the significance of ethylene and its accompanying molecular networks in ripening control. A major role of ethylene is to control fruit ripening, which includes softening tissues, releasing fragrance compounds, and converting starches to sugars. Aside from these, ethylene affects how plants respond to biotic and abiotic challenges such pathogen invasion, dehydration, and flooding, as well as other elements of plant growth like seed germination, root development, and floral senescence (Tucker et al., 2017).

There are several factors such as plant hormones, transcription factors, and epigenetic changes that are intimately related to provide a tight control of the ripening

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process. At the onset of ripening, climacteric fruits exhibit a large burst of respiration known as the "climacteric rise," along with a substantial and autocatalytic increase in the production of the gaseous hormone ethylene. The function of the respiratory climacteric is still unknown, but ethylene initiates and coordinates fruit ripening. The biosynthesis and perception of ethylene are tightly controlled, and the genes governing these processes are conserved among diverse plant taxa (Tang et al., 2020).

5.1. Hormonal regulations

The fruit ripening process can be influenced by three levels of regulations during fruit development which are hormonal regulations, transcriptional regulations and epigenetic regulation. Hormonal regulation denotes that the fruit ripening process is controlled through hormones present in the fruit or through external hormone applications. According to Seymour et al. (2013a), ethylene is used in a large range of processes within plants which include (i) biotic and abiotic stresses, (ii) abscission and flowering and (iii) developmental regulation besides fruit ripening. Ethylene plays an important role in managing fruit ripening and is considered a ripening hormone that has the capability to induce fruit ripening in storage for the fruit itself or surrounding fruits, either climacteric or non-climacteric (Seymour et al., 2013b). Thus, during fruit storage, it is not advisable to store fruit with high ethylene production in the same place as the unripe fruits. Strawberry is an example of a non-climacteric fruit which shows a rising level of ethylene production during fruit ripening as the ethylene functions in regulating gene expression occurring in pectin metabolism, hemicellulose metabolism as well as galactan and arabinan metabolism to stimulate strawberry ripening (Anwar et al., 2021).

Furthermore, another phytohormone which is abscisic acid (ABA), is recognised to play a role in plant growth, development, and responses to environmental challenges. ABA stimulates the accumulation of sugar in fleshy fruits and regulates both climacteric and non-climacteric fruit ripening (Osorio et al., 2013). Abscisic acid (ABA) also induces ripening. There is past research that demonstrates an increase in ABA levels occurs during the ripening process in both climacteric and non-climacteric fruits (Li et al., 2022). Thus, if the gene that encodes the functional enzymes in ABA synthesis were to be knock-off or silenced, the metabolic pathway in fruit ripening will be greatly affected. Besides that, overexpression of auxin-conjugating enzyme (IAA-amido synthetase) reduces the formation of free Indole Acetic Acid (IAA) leading to an increase in ethylene sensitivity during the fruit development of tomatoes (Karlova et al., 2014). Other phytohormones affecting fruit ripening are brassinosteroids and gibberellin acid (GA) (Brumos, 2021).

5.2. Transcriptional regulations

Transcriptional regulation also occurs during non-hormonal fruit ripening as it involves the transcription of the genes to be expressed. According to Anwar *et al.* (2021), a MADS-box transcription factor known as Ripening Inhibitor (RIN) is a regulator that can be found in tomato ripening in an ethylene-dependent manner and ethylene-independent manner. This transcription factor has two functions which are interconnecting with the promoters and controlling the expression of modulators for fruit ripening. The important modulators are Colourless Non-Ripening (CNR) and Non-Ripening (NOR) (Li et al., 2022). Those three transcriptions factors then connect with other transcription factors in order to inflect fruit ripening. For example, RIN, NOR and CNR will control transcription factors AP2a expression which functions to hinder the synthesis and signalling of ethylene. However, the AP2a expression also prompts the synthesis of brassinosteroids, auxin metabolism, and cell wall metabolism through gene expression at the same time (Anwar et al., 2021). In tomatoes, the *S1NAC4* gene positively stimulates ethylene levels although it is not caused by ethylene. However, the *S1NAC1* gene negatively stimulates the ethylene, lycopene and carotenoid levels as well as induces cell wall metabolism (cell wall disruption) via the ABA-mediated pathway. It terminates ethylene expression by binding with the promoter of ethylene synthesis genes (Anwar et al., 2021; Li et al., 2022).

5.3. Epigenetic regulations

The term "epigenetics" was originally used in 1956 by C.H. Waddington to denote the existence of inheritance mechanisms that go beyond those covered by traditional genetics (Nobel, 2015). Today, epigenetics is widely used to describe modifications that cause variation between organisms of the same species or different species that are mitotically inherited without changes in the DNA sequence. As for epigenetic regulation in fruit ripening, the ripening of the fruit progress by regulating the availability of the chromatin and attaching transcription factors to the DNA.

Numerous proofs show that there is a heritable variation that occurs in the gene expression by epigenetic mechanisms and explained that the major effect of these changes that occur is due to methylation levels of DNA and alteration of the histones (Brumos, 2021; Li et al., 2022). This is because chromatin functions as genetic information carrier. Hence, the chromatin form and the genetic data it carried subsequently, will be affecting the gene transcription via DNA methylation and post-translational alteration of histone proteins (Li et al., 2022). Epigenetic regulations that are mostly recognized are histone modifications, DNA methylation and the role of non-coding RNAs (Li, 2021). The term epialleles is also used to describe epigenetic alleles that have different chromatin states and is a source of phenotype variation. There are many examples of epigenetic changes in different crops and is a source of new variation which can be used for future breeding programs (Hofmeister et al., 2017).

5.3.1 Histone modification

To understand the mechanism of histone modification, we must first understand chromatin in which histone plays a major part in the formation of its structure. Chromatin is formed from nucleosomes in which DNA is wrapped around an octamer of histone proteins. This structure acts as a barrier to transcription, replication and repair of the DNA. It also acts as a regulator for the production of proteins and enzymes necessary for the appropriate cellular pathways. Histones in nucleosomes, can be modified by several processes such as acetylation, methylation, phosphorylation and ubiquitinylation (Verdin & Ott, 2015; Ramirez-Prado, 2018).

Histone acetylation results in transcriptionally active DNA sequences. Acetylation is carried out by the histone acetyltransferase (HAT) enzyme, while deacetylation is caused by histone deacetylase (HDAC) enzyme which allows changes in epigenetic marks as acetylation can be removed by HDAC. Acetylation in the histone lysine residue changes the charge in the histone tails thus reducing the interaction between histones and DNA, allowing more access to transcription factors. Acetylation can also cause chromatin to become binding sites for complexes that can stimulate transcription (Simithy et al., 2017).

A histone deacetylases (HDAC) gene, *SlHDA1*, was isolated from tomato fruits and RNAi repression of that gene showed that *SlHDA1* acts as an inhibitor of fruit ripening by affecting ethylene synthesis and carotenoid accumulation. Ethylene content, ethylene biosynthesis genes and ripening-associated genes were significantly up-regulated in *SlHDA1* RNAi lines (Guo et al., 2017). A similar result was obtained with RNAi lines of *SlHDA3* which resulted in earlier ripening and increased carotenoid accumulation (Guo et al., 2018).

Methylation can occur in histones due to the histone lysine methyltransferases (HKMT). Depending on the histone that is methylated, this mechanism can also change gene expression by promoting or inhibiting transcription. Histone H3 lysine 9 dimethylation (H3K9me2) plays a role in histone modification of transcriptional gene silencing. Investigations in *Arabidopsis* revealed that H3K9me2 is catalysed by the histone methyltransferase SUVH4/KYP. Further results revealed that histone methylation caused the recruitment of the methyltransferase CMT3 to methylate DNA loci (He et al., 2011). Another example on the effect of histone modifiers in tomato is a study using bioinformatics approach and *S. pennellii* introgression line. Integration with the histone modifier's map position was carried out to investigate their expression profiles. The results showed candidate genes for carotenoid biosynthesis in tomato using the two data (Guo et al., 2016).

Other than acetylation and methylation, phosphorylation is also a type of modification to histones which is involved in DNA repair, chromosome segregation and cell division. Phosphorylation of histones is affected by epigenetic marks of adjacent histones. Another histone modification, ubiquitination, is involved in regulatory functions and can influence cell cycle, development and pathogen resistance (Pikaard & Scheid, 2014).

5.3.2 RNA interference

Another type of epigenetic modification is carried out by small RNAs which can affect gene expression without changing the DNA sequence. In general, the regulation of gene expression by small RNAs is also called RNA interference (RNAi) or Post-Transcriptional Gene Silencing (PTGS). The small RNAs target complementary mRNAs for degradation or translational repression in the cytoplasm (Matzke & Mosher, 2014).

The small RNAs are non-coding RNA, approximately 22 nucleotides long and act as a guide for post-transcriptional control of protein coding genes (Mocellin & Provenzano, 2004; Mallory et al., 2004). MicroRNAs (miRNAs) along with small interfering RNA (siRNA) are classes of non-coding RNA. They are RNAs that do not encode a protein but play an important role in the development of an organism and Figure 3 illustrates the reciprocal regulation of miRNAs and the epigenetic apparatus. The siRNAs and miRNAs are both short duplex RNA, the difference in that siRNAs are transcribed from cellular genes or infecting pathogens, or artificially introduced into the cells and miRNAs are transcribed from micro-RNA genes (MIR) genes. The regulation of both RNAs can be affected by environmental conditions (Lam et al., 2015; Neumeier & Meister, 2021, Tang et al., 2022)

The process of gene silencing by PTGS occurs in the cytoplasm and is caused by a short duplex RNA that can be double stranded or hairpin shaped. In the case of miRNAs, they are then processed by the RNase II enzymes Dicer or Dicer-like (DCL) protein into small RNA molecules with 20-24 nucleotides. The Dicer protein along with Argonaute (AGO) are the two core proteins involved in the process. The resulting small RNA (sRNA) molecules are formed into an RNA-induced silencing complex (RISC). The sRNA molecule guides the RISC to a complementary single stranded RNA and the Argonaute cleaves the RNA. If there is a mismatch between the small RNA molecule with the mRNA, the mRNA is not cleaved but gene silencing still occurs (Matzke & Mosher, 2014; Chuang & Jones, 2007; Guo et al., 2016).

In the nucleus, small RNAs regulate gene expression by directing epigenetic modifications such as methylation of cytosines and histone methylation. The mechanism where RNA is involved in the methylation of DNA is known as RdDM (RNA-directed DNA Methylation). The proteins DICER-like3 (DCL3), Argonaute4 (AGO4), the DNA dependent RNA polymerases (Pol IV and Pol V) and RNA-dependent polymerase RDR2 are involved in RdDM. In the process, the Domain Rearranged Methyltransferase 2 (DRM2) protein is directed to add methyl groups to cytosines within the target region (Lopez & Wilkinson, 2015; Baulcombe, 2004).

The role of miRNAs in the regulation of tomato fruit ripening has also been investigated. The 3’-UTR of *LeSPL-CNR* mRNA possesses a potential target site for micro RNAs: miRNA156 and miRNA157. MiRNA-based virus induced gene silencing (Mr VIGS) was used to express pre-SlymiR157. SlymiR157 was found to regulate the *LeSPL-CNR* gene in a dose-dependent manner through miRNA-induced mRNA degradation and translation repression. This caused a delayed ripening effect in tomato fruit. A related miRNA, SlymiR156, affects fruit softening tomato after the red ripe stage (Chen et al., 2008). However, recent studies show that the roles of SlymiR156 and SlymiR157 still need to be investigated and proven, as many tomato miRNAs are discovered and show the many roles that they play in the development of the tomato plant (Arazi & Khedia, 2022).

5.3.3 DNA methylation

Cytosine methylation in the plant genome is modulated by the coordination of several gene products and these include DNA methyltransferases, DNA demethylases, histone-modifying or remodelling enzymes and RNAi components (Teixeira et al., 2009). In plants, there are three DNA methyltransferases that have been identified. These are METHYLTRANSFERASE 1 (MET1), CHROMOMETHYLASE 3 (CMT 3) and DOMAINS REARRANGED METHYLASE 2 (DRM2) (He et al., 2011; Zhang et al., 2018). MET1 is a homolog of the mammalian DNMT1 DNA METHYL TRANSFERASE1 (DNMT1) which is responsible for the maintenance of symmetric CG methylation. CMT3 is needed for the maintenance of DNA methylation at CHG sites, while DRM2 is responsible for de novo DNA methylation at all CHH sites (Chen et al., 2008). There are other methyltransferases which still need to be characterized and these include those encoded by the genes *MET2a*, *MET2b* and *MET3*. Also, other *CMT* genes (*CMT1* and *CMT2*) and genes from the DRM class (*DRM1* and *DRM2*) (Martienssen & Colot, 2001).

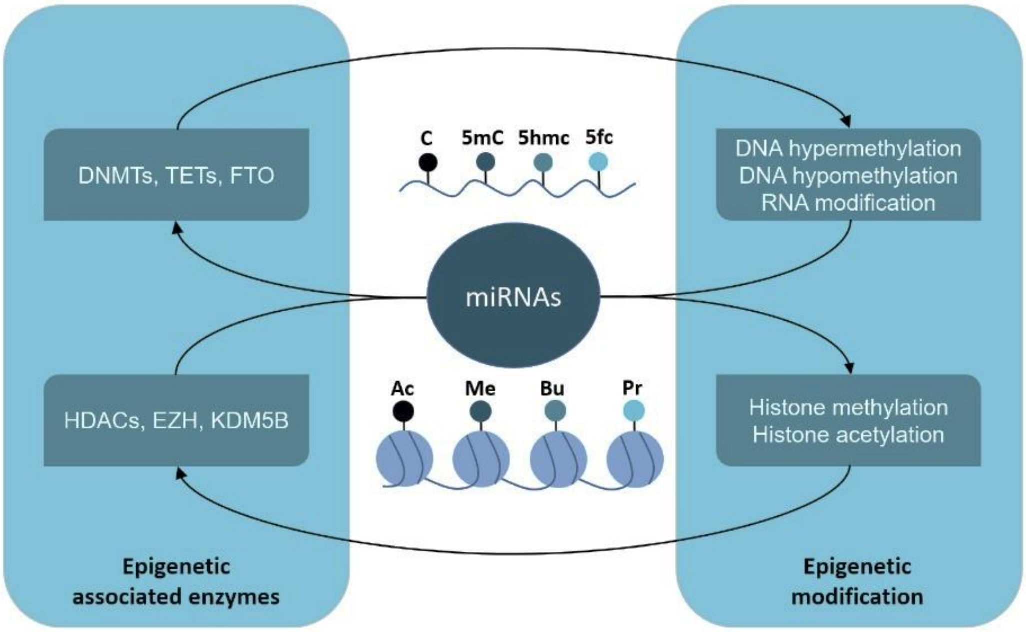

Figure 3: The miRNA-epigenetic loop is regulated by epigenetic regulators (DNA methylation, RNA modification, and histone modification). Epigenetics-associated enzymes are also under the control of miRNA regulation.

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The first plant gene encoding cytosine methyltransferase was isolated from *Arabidopsis*. The *Arabidopsis MET1* gene is a member of a small multigene family and MET1 is the predominant methyltransferase, being expressed in vegetative and floral tissues. MET1 homologues have been identified in a wide variety of plant species and the main role of MET1 is suggested to be in restoring parental pattern of cytosine methylation to the newly replicated DNA daughter strands (Finnegan & Kovac, 2000).

The discovery of the naturally occurring tomato epi mutant *Cnr* suggested that there was an important role of epigenetic regulation in fruit ripening (Manning et al., 2006). Investigations have shown that demethylation of ripening-related genes is important for tomato fruit developmental processes (Zhong et al., 2013; Liu et al., 2015). The role of methyltransferase in the methylation of the *CNR* promoter was investigated using 5-azacytidine which is an inhibitor of methyltransferase (Zhong et al., 2013). The inhibition caused premature ripening of tomato fruit. Additionally, it was also demonstrated that the promoters of ripening-related genes were demethylated at the onset of ripening in tomato. This study was supported by data from (Liu et al., 2015) who demonstrated that a *DEMETER-like* gene encoding a DNA demethylase was necessary for normal ripening in this fruit. It has also been shown that silencing of *chromomethylase3* (*SlCMF3*), can reduce methylation in the *LeSPL-CNR* promoter region and trigger normal fruit ripening (Chen et al., 2008). Other than DNA demethylase, an RNA demethylase known as ALKBH2 is known to regulate alterations of transcript methylation that were integrated with tomato fruit ripening process. This is done by the attachment of ALKBH2 and adjusting the DEMETER-LIKE 2 (DML2) stability. As a result, it initiates the relation of mRNA with DNA methylation leading to the promotion of fruit ripening (Javier, 2021).

6. CONCLUSION

In conclusion, tomato has become one of the world's most significant vegetable crops. Development of the plant's molecular biology, coupled with its genome sequencing and the study of wild relative species, has enabled researchers to surpass the limits of classical methodology of study, particularly in breeding, determining the tomato's ancestor, manipulating the genome for commercial value, and comprehending the fruit ripening mechanism.

Although ethylene plays a critical role in fruit ripening, there is insufficient evidence to directly relate it to epigenetics. Nevertheless, some research indicates that the expression of genes involved in ethylene signalling and fruit ripening may be influenced by epigenetic processes such DNA methylation and histone changes. Fruit ripening timing and extent can be influenced by these epigenetic alterations, which can affect the activity of genes linked to ethylene biosynthesis, perception, and response. Thus, although ethylene continues to be the predominant catalyst for fruit ripening, ethylene-related gene expression pathways may be modulated by epigenetic mechanisms.

It is intriguing to imagine that species' adaptation to their surroundings may include new methylation, which is then passed forward. It can also be hypothesized that the species' adaptation to their environment may include novel methylation which is then passed forward in the next generation. This is an essential aspect that might have a big influence on breeding strategies for crop improvement. In the future, heritable variation other than changes in gene sequences will be crucial to consider as a foundation for molecular methods to selection.

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