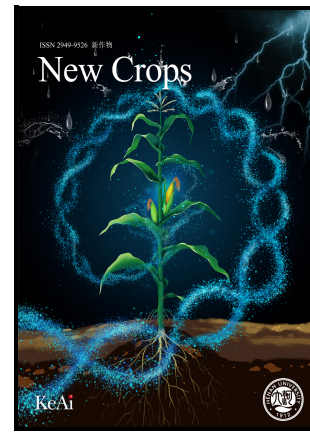


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PII: S2949-9526(24)00034-7

DOI: <https://doi.org/10.1016/j.ncrops.2024.100044>

Reference: NCROPS100044

To appear in: *New Crops*

Received date: 27 June 2024

Revised date: 1 August 2024

Accepted date: 18 August 2024

Please cite this article as: Marianne Delarue, Moussa Behnamed and Sotirios Fragkostefanakis, The role of epigenetics in tomato stress adaptation, *New Crops*, (2024) doi:<https://doi.org/10.1016/j.ncrops.2024.100044>

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## The role of epigenetics in tomato stress adaptation

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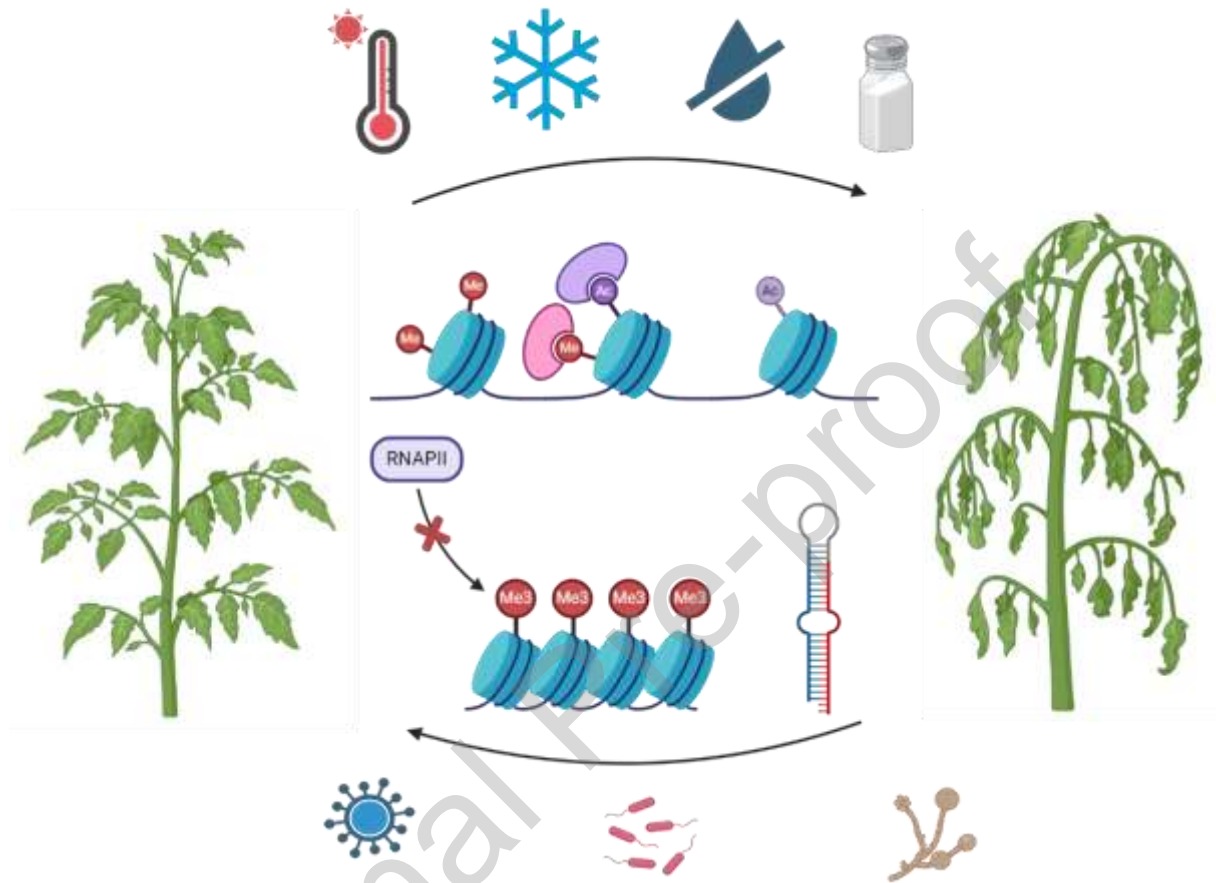
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### Abstract

Climate change poses a major challenge to agriculture, affecting crop production through shifting weather patterns and an increase in extreme conditions such as heat waves, droughts, and floods, all of which are further compounded by biotic stress factors. Tomatoes, a vital dietary staple and significant agricultural product worldwide, are particularly susceptible to these changes. The need for developing climate-resilient tomato varieties is more urgent than ever to ensure food security. Epigenetic modifications, such as DNA methylation and histone modifications, play essential roles in gene expression regulation. These modifications can affect plant traits and responses to environmental stresses, enabling tomatoes to maintain productivity despite variable climates or disease pressures. Tomato, as a model plant, offers valuable insights into the epigenetic mechanisms underlying fruit development and responses to stress. This review provides an overview of key discoveries regarding to tomato response and resilience mechanisms related to epigenetics, highlighting their potential in breeding strategies to enhance tomato resilience against both abiotic and biotic challenges, thereby promoting sustainable agricultural practices in the context of global climate change.

## Graphical abstract



**Keywords:** epigenetics, tomato, DNA methylation, histone modification, biotic, abiotic, stress

## Introduction

Climate change is one of the greatest challenges of the 21st century, profoundly impacting agriculture by altering growing conditions and posing significant threats to crop production. Rising temperatures, unpredictable weather, shifting precipitation patterns, and more frequent extreme events like heat waves, droughts and floods are direct consequences of climate change that negatively affect crops. These stressors can lead to reduced yields, diminished crop quality, and heightened vulnerability to pests and diseases. The resulting fluctuations in food supply pose a serious threat to global food security. As a result, developing climate-resilient crop varieties and adopting sustainable agricultural practices have become crucial to securing future food supplies.

Tomatoes are a staple in the human diet and among the world's most valuable crops, both nutritionally and economically (Cammarano *et al.*, 2022). Rich in vitamins C and K, potassium, folate, and antioxidants such as lycopene, they are essential to a healthy diet and have been associated with a reduced risk of heart disease and cancer.

The cultivated tomato, *Solanum lycopersicum*, was originally domesticated in Western South and Central America (Blanca *et al.*, 2015). It belongs to the division Magnoliophyta, class Magnoliopsida, subclass Asteridae, order Solanales, and family Solanaceae (Fernandez-Pozo *et al.*, 2015). Botanically classified as a fruit (specifically a berry), the tomato is commonly consumed as a vegetable. Although it is a tropical plant, it can adapt to various climates worldwide. The leading tomato-producing countries include China, the USA, India, Turkey, Egypt, and Italy (Costa & Heuvelink, 2018). The tomato is a diploid species with a chromosome number of  $2n = 2x = 24$ . It exhibits a range of growth habits from determinate to indeterminate and has bisexual flowers (Fernandez-Pozo *et al.*, 2015). Typically, tomatoes are self-pollinated and propagated via seeds. Globally, over a thousand cultivars are grown, selected based on fruit size, shape, and adaptability to different environments (Blanca *et al.*, 2015).

Tomato cultivation, whether in open fields or greenhouses, faces various stresses that can significantly impact plant health and productivity (Costa & Heuvelink, 2018). Achieving optimal yield and fruit quality requires balancing several environmental factors. The ideal conditions for tomato growth include long daylight hours and an optimal temperature range of 20°C to 25°C (Costa & Heuvelink, 2018). Appropriate soil conditions, water management, air circulation, mechanical support, and nutrition are essential for tomato cultivation to avoid abiotic and biotic stresses, ensure healthy and robust plants, and ultimately high yields and superior fruit quality.

Tomato has undergone extensive breeding efforts aimed at enhancing traits such as yield, disease resistance, and fruit quality, using both traditional and molecular breeding techniques (Blanca *et al.*, 2015). Recent advances in genomics have allowed breeders to identify key genetic variations and use marker-assisted selection to streamline the breeding process, significantly improving efficiency and precision (Wang *et al.*, 2024).

Epigenetics involves reversible and heritable changes in gene expression that occur without alterations in the DNA sequence itself. These changes driven by modifications such as DNA methylation and histone alterations (Gallusci *et al.*, 2017). Epigenetic changes can influence plant traits, and in tomato, they have been linked to fruit growth and ripening, as well as the plant's response and resilience to abiotic and biotic stresses (Guarino *et al.*, 2022). Therefore,

epigenetics can enable the development of tomato varieties that maintain high productivity despite fluctuations in climate or susceptibility to diseases. In addition, the tomato serves as a model plant for studying fleshy fruit development, climacteric ripening, plant-pathogen interactions, and abiotic stresses within Solanaceae family (Tomato & Consortium, 2012; Liu *et al.*, 2022d). Given the abundance of epigenetic studies on tomato, this review summarizes key findings related to abiotic and biotic stresses, aiming to offer a roadmap for exploring the role of epigenetics in tomato breeding.

### **An overview of epigenetic mechanisms in plants**

Epigenetic mechanisms in plants involve complex modifications that do not alter the DNA sequence itself but instead affect gene expression. These modifications can be inherited in some cases through cell divisions (Gibney & Nolan, 2010). One key epigenetic modification is DNA methylation, which involves the addition of a methyl group to DNA, typically at cytosine bases. In plants, DNA methylation occurs in three contexts: CG, CHG, and CHH (H represents A, T, or C) (Rutowicz *et al.*, 2015). These methylation patterns can be stable and inherited, providing a mechanism for environmental memory in plants (Ibañez & Quadrana, 2023). Histones, the protein components of chromatin, undergo various post-translational modifications that influence their interaction with DNA and nuclear proteins, thereby regulating DNA accessibility and gene expression (Deal & Henikoff, 2011). Common modifications include methylation, acetylation, phosphorylation, and ubiquitination. Each of these modifications can either promote or inhibit gene expression depending on the type and location of the modification. For instance, methylation of histones H3K9 and H3K27 generally correlates with repressed gene expression, whereas acetylation of histones is associated with transcriptional activation (Asensi-Fabado *et al.*, 2017). Additionally, the dynamic modification of chromatin architecture can either expose or conceal DNA from the transcriptional machinery. Changes in nucleosome positioning and density can influence the accessibility of transcription factors to DNA, thus affecting gene expression patterns during development and in response to stress (Lämke & Bäurle, 2017).

Furthermore, RNA-mediated modifications contribute to epigenetic regulations, with small non-coding RNAs, such as short interference RNAs (siRNAs) and microRNAs (miRNAs), playing key roles in affecting DNA methylation patterns and histone modifications (Manavella *et al.*, 2023). These small RNAs can guide silencing complexes to specific genomic regions, leading to altered chromatin states and suppression of gene expression, making them crucial for fine-tuning plants' responses to stress and developmental processes. Additionally, long non-

coding RNAs (lncRNAs) modulate gene expression at various levels, including chromatin modification and transcriptional control. Acting as scaffolds, guides, or decoys, lncRNAs interact with chromatin modifiers, thereby influencing the epigenetic landscape (Ariel *et al.*, 2015).

### **Epigenetic mechanisms in tomato in Response to abiotic stresses**

Several epigenetic mechanisms are involved in the response of tomato plants to abiotic stresses, including short acute treatments that have long been used to extend shelf life. An overview is provided in Table 1, with examples illustrated in Figure 1.

#### **Heat stress**

Exposure to temperatures 10°C -15°C above the optimal range for growth and development, which commonly occur during warmer periods of the year, cause heat stress (HS) (Alsamir *et al.*, 2021). Heat-stressed plants exhibit reduced growth and altered organ morphology, with developmental transitions such as flowering being either accelerated or delayed. At the cellular level, high temperatures can cause membrane damage, protein misfolding and aggregation, and the inactivation of key enzymes essential for processes such as photosynthesis and respiration (Wahid *et al.*, 2007). Survival under heat stress primarily depends on a global metabolic reprogramming of the cell that prioritizes the synthesis of proteins with protective functions (Bokszczanin *et al.*, 2013; Tiwari *et al.*, 2023).

Tomato plants are highly sensitive to heat stress, with most varieties struggling to grow well at temperatures above 38°C (Alsamir *et al.*, 2021). Since temperature increases above the optimum often occur late in the growing season for tomatoes, reproductive traits that directly impact final yield are influenced by various factors. These include transcriptional factors, heat shock proteins, peptides related to flowering, processes like pollen and fruit set, some of which may be regulated epigenetically (Graci & Barone, 2023; Liu *et al.*, 2023).

DDM1 is a SWI2/SNF2 (SWItch/Sucrose NonFermentable2) chromatin remodeling protein that enables DNA methyltransferases to access heterochromatin, thereby facilitating DNA methylation (Zemach *et al.*, 2013). A tomato mutant deficient in DNA methylation exhibits a thermotolerance phenotype under heat stress (HS) compared with the wild type (WT) control line, characterized by higher fruit set and seed set rates, as well as altered expression of HS-related genes (Singh *et al.*, 2021). These findings are consistent with those in the model plant *Arabidopsis thaliana*, where the HS-induced transcriptional activation of loci within

heterochromatic chromatin is hyperactivated and persists longer in the *ddm1* single mutant than in the WT (Iwasaki & Paszkowski, 2014).

Transcription factors (TFs) play a crucial role in regulating downstream genes by binding to cis-elements in gene promoters, thereby controlling plant response and tolerance to HS. Among the various transcription factors identified for their role in tomato heat tolerance, heat shock factors (HSFs) have garnered the most attention in research (Fragkostefanakis *et al.*, 2015; Ohama *et al.*, 2015). HSFs drive the transcriptional activation of HS-related genes, leading to the accumulation of heat shock proteins and reducing stress-induced damage (von Koskull-Döring *et al.*, 2007). In tomato, it has been reported that HSF1 recruits HISTONE ACETYLTRANSFERASE1 (HAC1) to chromatin, suggesting that the interaction between HSF1 and HAC1 regulates gene expression and contributes to HS tolerance (Bharti *et al.*, 2004). However, it remains unclear whether the enrichment of HAC1 at HS-regulated loci stimulates histone lysine acetylation. Recent studies have shown that HS triggers chromatin remodeling, leading to changes in interactions between promoters and distant regulatory elements (Huang *et al.*, 2023). In addition, research on the role of the HS master regulator HSF1a has revealed its critical involvement in the dynamic formation of promoter-enhancer contacts and in controlling the transcriptional response at the onset of HS (Huang *et al.*, 2023).

Numerous non-coding RNAs (ncRNAs) have been identified as important regulators in HS responses (Li *et al.*, 2023). Among them, miR319d plays a crucial role in regulating gene expression and conferring HS tolerance in tomatoes (Shi *et al.*, 2019). Comparative expression profiles of the *MIR169* family and its targets suggest *MIR169* acts as a ubiquitous regulator of various abiotic stresses, including heat, cold, dehydration and salt (Rao *et al.*, 2020). Tomato plants overexpressing this family have demonstrated enhanced thermotolerance, attributed to altered expression of several heat-related key genes, including *HSFA1a*, *HSFA1b* and *HSP90*. Notably, HS tolerance can be enhanced through HSF-mediated transcriptional regulation of *MIR169* and post-transcriptional regulation of Nuclear Factor-YA (NF-YA) transcription factors. HSF1a, HSF2 and HSF7a play key roles in HS response by binding to the promoters of *MIR169*, thereby enhancing its transcription. The increased accumulation of miR169s reduces NF-YA levels, which in turn boosts the expression of HS-related genes such as *HSFA2*, *HSFA3* and *HSFA7s*. This research highlights a feedback regulatory loop involving HSFs, miR169s and NF-YAs, which is critical in regulating the heat stress response in tomatoes (Rao *et al.*, 2022).

Additionally, hot water treatment is sometimes employed to delay fruit ripening and senescence (Loayza *et al.*, 2021). In response to this treatment, significant changes in the DNA methylation of genes involved in the ethylene signaling pathway have been identified, suggesting an impact on ethylene signal transmission that leads to a delay in the postharvest ripening of tomato fruit (Pu *et al.*, 2020).

### **Chilling injury**

Low temperature is a significant abiotic stress that negatively affects the growth, yield, and quality of crops. Many tropical and subtropical crops, such as tomato, rice, and maize, are particularly sensitive to low temperatures ranging from 0°C to 12°C and unable to tolerate freezing conditions (Thomashow, 1999). Chilling of tomato fruits leads to increased DNA methylation in the promoters of ripening-related genes, resulting in reduced expression and a decrease in ethylene biosynthesis (Zhang *et al.*, 2016).

On the other hand, 239 long non-coding RNAs (lncRNAs) have been shown to be differentially expressed in response to chilling stress (Wang *et al.*, 2018a). Numerous target genes were identified, many of which encode proteins related to chilling stress, including enzymes involved in redox reactions, energy metabolism and the metabolism of salicylic acid and abscisic acid (Wang *et al.*, 2018a).

Another layer of post-transcriptional epigenetic regulation involves RNA modification, such as N<sup>6</sup>-methyladenosine (m<sup>6</sup>A) methylation of transcripts, which can be dynamically regulated and significantly influence various aspects of RNA metabolism, including stability, splicing, nucleus-to-cytoplasm export, alternative polyadenylation, and translation (Hu *et al.*, 2019). Through combined analysis of differential expression transcripts related to chilling injury and m<sup>6</sup>A methylation patterns, 41 differential expressed transcripts were identified. These transcripts are involved in chilling injury and encode factors associated with the biosynthesis or signaling pathways of ethylene, auxin, gibberellins and salicylic acid, as well as heat shock proteins (Bai *et al.*, 2021).

Moderate low-temperature (MLT) stress induced pollen abortion in tomato, a phenotype resulting from the disruption of tapetum development and pollen exine formation, which is accompanied by reduced m<sup>6</sup>A levels in the anthers (Yang *et al.*, 2021). Differentially m<sup>6</sup>A enriched transcripts under MLT stress were identified, and they were primarily associated with lipid metabolism, adenosine triphosphatase (ATPase) activity, and ATP-binding pathways. These changes correlated with elevated levels of abscisic acid (ABA) in the anthers and disrupted pollen wall formation under low-temperature stress (Yang *et al.*, 2021).



In addition, it has been demonstrated that tomato resistance to chilling stress is significantly enhanced by coronatine treatment, a phytotoxin that mimics the structure and function of (3R,7S)-jasmonoyl-L-isoleucine (JA-Ile), the bioactive form of plant hormone Jasmonic Acid (JA) (Liu *et al.*, 2022c). At a molecular level, coronatine influences the methylation of histone H3 on the lysine 4 (H3K4me3) in C-repeat-Binding Factor (CBF)-type transcription factors, which are induced in response to cold stress. These modification increases chromatin accessibility, leading to improved resistance to chilling stress (Liu *et al.*, 2022c).

### **Drought Stress**

Cultivated tomato varieties are highly sensitive to water deficiency, making drought a devastating factor for fruit yield. Drought affects plant-water relations and generates reactive oxygen species (ROS), leading to the abortion of floral buds and open flowers, as well as germination failure. This sensitivity is primarily due to the vulnerability of the male gametophyte (Lamin-Samu *et al.*, 2021; Xie *et al.*, 2024).

A comparative analysis of the expression of drought response genes in cultivated tomato and at least two drought-resistant members of the *Solanum* genus (i.e. *S. pennellii* Corr. and *S. chilense* Dun) revealed differential expression of a gene encoding a putative Histone H1 in response to ABA and drought stress (Kahn *et al.*, 1993; Wei Tao & O'Connell, 1996). Similarly, the histone variant H1 (HI-S) specifically accumulates in tomato leaves subjected to water-deficit conditions (Scippa *et al.*, 2000). Although the functionality of H1 histones in response to drought stress has not been clearly demonstrated, the loss of function of two histone deacetylases, SIHDA1 and SIHDA3, leads to hypersensitivity to water and salt stress in RNAi transgenic lines (Huang *et al.*, 2016; Guo & Wang, 2023; Guo *et al.*, 2023). These two enzymes play a role in the positive regulation of abiotic stress tolerance, likely through the modification of histone acetylation in target genes, and may represent new target genes for engineering salt- and drought-tolerant tomatoes.

Another notable drought-stress response gene is *ASR2* (named after ABA, Stress, Ripening2), which has undergone positive selection during the evolution of the *Solanum* genus in arid environments (Frankel *et al.*, 2006). A brief exposure to simulated drought conditions resulted in the removal of methylation DNA marks in the regulatory region of the *ASR2* gene. Additionally, under normal conditions, both the regulatory and coding regions contained the typically repressive H3K9me2 mark, which was lost after 30 minutes of water deprivation. This loss was correlated with the removal of DNA methylation, both changes being inversely associated with *ASR2* gene expression (González *et al.*, 2013).

Similarly, mutations in histone H3 lysine methyltransferases Set Domain Group 33 (*SDG33*) and *SDG34* reduce susceptibility to biotic and abiotic stress by disrupting the permissive transcriptional context that promotes the expression of negative regulatory factors in stress response. Interestingly, single mutants exhibited tolerance to drought, while the double mutant showed superior tolerance, consistent with the independent and additive functions of both histone methyltransferases (Bvindi *et al.*, 2022b). Additionally, HDA5-silenced tomato plants displayed increased sensitivity to ABA treatment and reduced tolerance to drought and salt stress, wilting and dehydrating earlier than the wild type. This was further confirmed by lower water and chlorophyll content in the transgenic plants (Yu *et al.*, 2018).

In plants, small interfering RNAs (siRNAs) are known to guide DNA methyltransferases to siRNA-generating genomic loci and other loci for de novo DNA methylation, a pathway known as RNA-directed DNA methylation (RdDM). This pathway causes fluctuations in the expression levels of stress-related genes, thereby enhancing stress tolerance in plants (Lu *et al.*, 2024).

One of the key players in the RdDM pathway is the Dicer-like protein AGO4. In tomato, *SIAGO4A* knock-down transgenic plants demonstrated enhanced tolerance to salt and drought stress compared to the wild type, as evidenced by seed germination rate, primary root length, and higher chlorophyll, proline, and soluble sugar content (Huang *et al.*, 2016). Notably, the expression levels of certain DNA methyltransferase genes and RNAi pathway genes were significantly lower in the knockdown plants, suggesting that the *SIAGO4A* gene plays a negative role under salt and drought stress, likely by modulating of DNA methylation as well as the classical RNAi pathway (Huang *et al.*, 2016).

Various mechanisms have evolved to protect plant genomes, including the suppression of Transposable Elements (TE) transcription through epigenetic silencing, which restricts TE movement and accumulation. The RdDM pathway is also crucial for controlling transposons activity. In tomato, transpositions of the LTR (long terminal repeat) retrotransposon family Rider have contributed to various phenotypes of agronomic interest, such as fruit shape, color, and abiotic stress tolerance (Benoit *et al.*, 2019). The accumulation of Rider transcripts and transposition intermediates in the form of extrachromosomal DNA is triggered by drought stress and is dependent on abscisic acid signaling (Benoit *et al.*, 2019).

At the post-transcriptional level, analyses of the lncRNA transcriptome landscape in tomato anthers under drought stress identified several drought-responsive lncRNAs. Functional enrichment and co-expression analysis revealed that the target genes of these lncRNAs were

significantly enriched in various metabolic processes, including carbohydrate metabolism and hormone synthesis (ABA and JA) highlighting the potential role of lncRNA–target gene modulation in anther development under drought stress (Lamin-Samu *et al.*, 2021, 2022). Additionally, expression pattern and functional analysis of potential mRNA targets in leaves suggested that drought-responsive tomato lncRNAs play crucial roles in a variety of biological processes via lncRNA–mRNA co-expression (Eom *et al.*, 2019).

Epigenetic mechanisms also play a role in the response of tomato plants to grafting. Self-grafting in tomato plants led to changes in histone and DNA modifications associated with alterations in gene expression. One week after self-grafting, changes in H3K4me3 and H3K27me3 marks were observed in over 500 genes for each modification, while DNA methylation changes were noted in more than 5,000 genomic regions at the shoot apex compared to non-grafted controls (Fuentes-Merlos *et al.*, 2023). In addition, two weeks after these epigenomic modifications, global expression changes continued to be observed at the shoot apex in several genes related to nitrogen compound metabolism, responses to stimuli, chromosome organization, the cell cycle, and hormone level regulation. Remarkably, these grafted seedlings exhibited enhanced drought tolerance, suggesting that epigenomic modifications during the wound-healing process contribute to increased stress tolerance in tomato plants (Fuentes-Merlos *et al.*, 2023).

### **Salinity stress**

Plants experience salinity stress due to the accumulation of water-soluble salts, primarily sodium (Na<sup>+</sup>), potassium (K<sup>+</sup>), chloride (Cl<sup>-</sup>) or sulfate (SO<sub>4</sub><sup>2-</sup>), in the rhizosphere. Salinity primarily causes osmotic stress, limiting water uptake, but in the long term, it also leads to toxicity due to ion imbalance and the accumulation of Cl<sup>-</sup>, which further induces secondary stresses such as oxidative stress and changes in metabolic homeostasis (Guo *et al.*, 2022). As a result, there is a significant overlap between drought and salinity stress (Huang *et al.*, 2016; Yu *et al.*, 2018; Guo & Wang, 2023; Guo *et al.*, 2023).

An initial indication of specific epigenetic responses to salt stress was provided by an exhaustive analysis of the expression of genes coding for DNA methyltransferases (DMTs). Seven out of nine tomato DMTs are differentially expressed in tomato plants exposed to salt stress, suggesting that these DMT genes play a role in the salt stress response (Guo *et al.*, 2020). A key example involves the tomato proline-, lysine-, and glutamic-rich type factor PKE1, whose expression is regulated by its methylation level. This factor, isolated from abiotic-resistant

species, was overexpressed in tomato and tobacco, leading to enhanced salt tolerance (Li *et al.*, 2019).

Among the nine tomato HDA genes (named as *HDA1-HDA9*), the expression levels of *HDA1*, *HDA4*, and *HDA9* in root and *HDA3* in leaf were significantly upregulated by salt treatment. Additionally, *HDA2*, *HDA5*, and *HDA6* were induced in both roots and leaves (Guo *et al.*, 2017). As mentioned earlier, the *HDA5*-silenced tomato plants exhibited reduced tolerance to salt stress (Yu *et al.*, 2018).

S-adenosylmethionine (SAM), synthesized from methionine and ATP by S-adenosylmethionine synthetase (SAMS), serves as a crucial methyl donor and plays a significant role in plant responses to abiotic stresses, particularly salt stress. Previous research indicated that SAMS enhances salt tolerance in tomato plants, but the involvement of the DNA methylation pathway in this process was unclear (Zhang *et al.*, 2020). Recently, it was confirmed that tomato plants overexpressing *SISAMS1* showed improved salt tolerance through the regulation of the *SIG1* gene (an orthologue of *GIGANTEA*), identified in a whole genome analysis. Overexpressing of *SISAMS1* led to significant changes in CHG-type methylation sites within the *SIG1* gene body and altered its expression levels, thereby enhancing salt tolerance (Chen *et al.*, 2023).

Compared to cultivated tomato, the wild tomato *S. pennellii* displays significantly greater salt tolerance. High-throughput sequencing comparative analyses between these two varieties identified differentially expressed lncRNAs. Functional analysis of the target genes of these differentially expressed lncRNAs (DE-lncRNAs) revealed that some genes respond positively to salt stress by participating in ABA, brassinosteroid and ethylene signaling pathway, as well as in anti-oxidation processes. This has enabled the construction of a salt-induced lncRNA-mRNA co-expression network, helping to elucidate the potential mechanisms underlying the high salt tolerance in *S. pennellii* (Guo *et al.*, 2022).

### **Nutrient deficiencies and heavy metal stress**

Nitrogen is an essential macronutrient for plants and a key factor limiting plant growth. In response to nitrogen availability, genome-wide changes in either permissive or repressive histone marks were analyzed in an organ-specific manner. Integration of transcriptomic and epigenomic datasets generated from the same organ revealed highly significant correlations between changes in transcript levels and histone modifications, with specific features

depending on the organ context (Julian *et al.*, 2023). This aligns with a previous study showing that two different histone methyltransferases can regulate nitrogen-responsive gene expression and physiological changes in an organ-specific manner (Bvindi *et al.*, 2022b).

Regarding stress linked to phosphate starvation, an integrative analysis of the methylome and transcriptome of tomato seedlings under phosphate -deficient and sufficient conditions showed that alterations in DNA methylation only weakly correlate with transcription changes. Moreover, hypermethylated regions, which primarily overlap with transposable elements (TEs), were enriched in a subset of phosphate - response genes. This suggests that most changes in DNA methylation likely regulate the expression of nearby TEs rather than directly affecting gene transcription (Zeng *et al.*, 2021).

Low potassium (K) stress activates various signaling molecules in plant cells, including reactive oxygen species (ROS),  $Ca^{2+}$ , plant hormones, and microRNAs (miRNAs). Comparative analyses of miRNA-seq between low-K tolerant JZ34 and low-K sensitive JZ18 tomato genotypes identified miRNA168 as differentially expressed (Xian *et al.*, 2014). miRNA168 was confirmed to target the *Argonaute1* (*AGO1*) in tomato, modulating the small RNA regulatory pathway via RNA silencing complex (RISC) (Wang & Wu, 2017). Transgenic tomato plants constitutively expressing *pri-miR168a* showed enhanced root system growth, improved leaf development, and higher potassium contents in the roots under potassium-deficiency stress compared to wild-type (WT) plants. Deep sequencing analysis showed that 62 known miRNAs were down-regulated in the transgenic line carrying the *CaMV35S:SlmiR168a* expression cassette compared to the WT plants. Integrated analysis identified several miRNA/mRNA pairs involved in the response to low-K stress, including pathways related to cytokinins, ABA and root growth modulation (Liu *et al.*, 2020).

Cadmium (Cd) is a non-essential metal and a major environmental pollutant that adversely affects various aspects of plant metabolism and development, including growth, transpiration, photosynthesis, respiration and nutrient distribution (Sanità Di Toppi & Gabbrielli, 1999). Investigating the molecular mechanisms involved in the response to Cd in tomatoes, it has been found that overexpression of the histone demethylase *JUMONJI-C DOMAIN-CONTAINING PROTEIN524* (*SIJM524*) enhances resistance to Cd stress. This is achieved by regulating the expression of metal transporter and Cd chelation pathway genes, as well as the genes involved in flavonoids synthesis (Li *et al.*, 2022).

## Epigenetic mechanisms related to biotic stresses in tomato

An overview of the epigenetic mechanisms related to the response of tomato to biotic stress factors is provided in Table 2, with examples shown in Figure 1.

### Fungal diseases

Tomato faces significant threats from fungal pathogens, which can severely impact both yield and quality (Table 2). Among these, the oomycete pathogen *Phytophthora infestans* causes late blight, one of the most devastating diseases for both tomato and potato (Nowicki *et al.*, 2012). Several studies have identified changes in coding and non-coding RNAs that might be associated with resistance to *P. infestans*.

Some lncRNAs function as competing endogenous RNAs (ceRNAs) by sequestering miRNAs, preventing them from downregulating their target mRNAs. In tomato, lncRNA08489 acts as a ceRNA for miR482e-3p, leading to increased expression of the *NBS-LRR* gene, a known resistance gene, thereby enhancing the plant's immune response (Liu *et al.*, 2022a).

Among 148 differentially expressed lncRNAs in tomato infected with *P. infestans*, 20 lncRNAs were identified as ceRNAs that decoy 11 miRNAs (Cui *et al.*, 2020). Specially, lncRNA42705/lncRNA08711, lncRNA39896, and lncRNA11265/lncRNA15816 decoy miR159, miR166b, and miR164a-5p, respectively, potentially regulating transcription factors from the MYB, HD-Zip, and NAC gene families. Tomato plants with silenced lncRNA42705 and lncRNA08711 showed increased levels of miR159 and decreased levels of MYB, respectively (Cui *et al.*, 2020). lncRNA16397 has been shown to confer resistance to *P. infestans* as overexpression of lncRNA16397 enhances the expression of glutaredoxin genes such as *SIGRX21* and *SIGRX22*, thereby reducing reactive oxygen species (ROS) accumulation and cell membrane damage during infection (Cui *et al.*, 2020). Similarly, overexpression of SllncRNA47980 improves ROS scavenging and alters phytohormone levels, reducing gibberellin (GA) and salicylic acid (SA) while increasing jasmonic acid (JA) (Su *et al.*, 2023). In contrast, silencing SllncRNA47980 reversed these effects. SllncRNA47980 regulates the *SIGA2ox4* gene, affecting GA content and plant immunity.

Overexpression of *SIMIR482e*, SlmiR482e-3p, and SlmiR482e-5p in transgenic plants increased susceptibility to *P. infestans*, while silencing these miRNAs enhanced pathogen resistance (Liu *et al.*, 2022b). Additionally, overexpression of SllncRNA39298 inhibited SlmiR482e-5p and increased resistance to *P. infestans*. Notably, ROS levels were elevated in

plants overexpressing the miRNAs and reduced in those overexpressing SlincRNA39298 compared to WT plants (Liu *et al.*, 2022b).

SlincRNA20718 acts as a positive regulator by reducing SlmiR6022 expression, thereby enhancing disease resistance through increased *PR* gene expression and reduced lesion size (Zhang *et al.*, 2024). In contrast, SlmiR6022 negatively affects resistance by targeting receptor-like protein genes (SIRLP6/10), leading to increased ROS and decreased levels of JA and ethylene. A six-point mutation in the pairing region of SlincRNA20718 and SlmiR6022 confirmed the role of SlincRNA20718 as an endogenous target mimic (eTM), sequestering and silencing SlmiR6022 (Zhang *et al.*, 2024).

Overexpression of lncRNA23468 in tomato led to reduced miR482b levels and increased expression of *NBS-LRR* genes, thereby enhancing resistance to *P. infestans*. Conversely, silencing lncRNA23468 reduced resistance (Jiang *et al.*, 2019). Mutation of the eTM site on lncRNA23468 did not affect miR482b or *NBS-LRR* levels. Silencing *NBS-LRR* resulted in plants exhibiting more severe disease symptoms, similar to those observed when lncRNA23468 was silenced (Jiang *et al.*, 2019). These findings underscore the critical role of lncRNAs as eTMs in modulating miRNA activity and contributing to tomato's defense against *P. infestans*.

The relationship between histone epigenetic marks and lncRNAs has also been explored in the responses of Arabidopsis and tomato to the necrotrophic pathogen *Botrytis cinerea*. Chromatin immunoprecipitation analysis revealed changes in histone marks, such as H3K4me3, H3K9ac, and H3K27me3, associated with gene responsiveness in Arabidopsis infected with *B. cinerea* (Crespo-Salvador *et al.*, 2018). H3K9ac levels increased on early-induced genes related to the oxylipin pathway and hormonal signaling during *B. cinerea* infection (Crespo-Salvador *et al.*, 2018, 2020). The distribution of H3K9ac differs significantly from that of H3K4me3, indicating a distinct epigenetic pattern. H3K9ac is associated with the early-induced genes such as *SIDES*, *SIDOX1*, and *SILoxD*, which code for enzymes involved in the oxylipin-pathway, as well as *SIWRKY75*, which codes for a transcriptional regulator of hormonal signaling (Crespo-Salvador *et al.*, 2020). The same study showed that the intron-binding miR1127-3p regulates *SIWRKY75*, and the reduction of this miRNA occurs in response to *B. cinerea* infection. Interestingly, H3K4me3 modifications at the miRNA binding site in response to *B. cinerea* may be related to the activity of miR1127-3p (Crespo-Salvador *et al.*, 2020).

Genes such as *PRI*, *CYP71A13*, and *EXL7* showed differential enrichment of these histone marks, indicating their involvement in plant defence. In tomato, the enrichment of H3K4me3 in the promoter and the gene body of several *B. cinerea*-responsive genes was observed.

Notably, *LoxD* was among these genes, which has been identified as a marker for the JA-pathway in tomato's resistance to *B. cinerea* (Finiti *et al.*, 2014).

lncRNA4504 is involved in methyl jasmonate (MeJA)-induced resistance to *B. cinerea* in postharvest tomato fruit (Crespo-Salvador *et al.*, 2018). MeJA treatment enhanced disease resistance, increased phenolic and flavonoid content, and boosted the activity of defensive enzymes, which was associated with the upregulation of JA pathway genes. However, silencing lncRNA4504 repressed the beneficial effects of MeJA, indicating that lncRNA4504 is crucial for MeJA-mediated defence enhancement against *B. cinerea* (Crespo-Salvador *et al.*, 2018).

The H2B monoubiquitination E3 ligases, *SIHUB1* and *SIHUB2* are induced by *B. cinerea* infection and treatments with SA and the ethylene precursor 1-amino cyclopropane-1-carboxylic acid (ACC) (Zhang *et al.*, 2015). Silencing *SIHUB1* or *SIHUB2* in tomato plants increased their susceptibility to *B. cinerea*. This silencing also resulted in higher levels of ROS and callose, as well as upregulation of genes involved in the phenylpropanoid pathway and SA-mediated signaling pathway following *B. cinerea* infection. Additionally, the tomato histone H3 lysine methyltransferases *SET Domain Group 33 (SDG33)* and *SDG34* exhibit alterations in H3K36 and H3K4 methylations and the expression of genes involved in biotic stress responses. The double mutant for these methyltransferases showed increased resistance to *B. cinerea* (Bvindi *et al.*, 2022a).

The rhizobacterial strain *Bacillus subtilis* SL18r induces systemic resistance in tomato against the foliar pathogen *B. cinerea* (Zhou *et al.*, 2021). This resistance is partly mediated through the activation of the lncRNA MSTRG18363, which acts as a decoy for miR1918, a microRNA that negatively regulates tomato immune responses. When tomato plants are inoculated with SL18r, MSTRG18363 expression increases, leading to a decrease in miR1918 levels and an increase in the expression of *SIATL20*, a gene targeted by miR1918 (Zhou *et al.*, 2021). Consequently, overexpression of *MSTRG18363* enhances disease resistance, while its silencing weakens it.

### **Bacterial infections**

Key bacterial pathogens affecting tomatoes include *Pseudomonas syringae*, which causes bacterial speck; *Xanthomonas* spp., responsible for bacterial spot; and *Ralstonia solanacearum*, known for causing bacterial wilt. These pathogens can invade tomato plants through natural openings or wounds, with their spread facilitated by factors such as high humidity and warm temperatures. An overview of the epigenetic mechanisms involved in tomato plants responses to bacterial infections is provided in Table 2.



RNA sequencing of tomato plants inoculated with *Ralstonia solanacearum* identified 315 potential long intergenic non-coding RNAs (lincRNAs), 23 of which were differentially expressed compared to uninfected plants (Cao *et al.*, 2022). Many of these lincRNAs were predicted to target genes involved in JA and ethylene signaling pathways, which are key components of the plant's response to bacterial wilt.

Comparative analysis of mRNA, lincRNA, and miRNA interactions in resistant and susceptible tomato lines inoculated with *R. solanacearum* identified 7506 mRNAs, 997 lincRNAs, and 69 miRNAs, which exhibited genotype-specific responses (Si *et al.*, 2023). Noncoding RNAs were predicted to regulate receptor-like kinases and cell wall synthesis. A ceRNA network suggested that SlmiR482e-3p and its potential eTMs may influence tomato susceptibility to this bacterial pathogen.

### **Viral infections**

Several studies have uncovered various epigenetic mechanisms that tomatoes use to defend against viral infections, particularly focusing on geminiviruses (Wang *et al.*, 2019). Plant RNA silencing systems play a crucial role in regulating gene expression and providing defense against viral infections (Table 2).

The Tomato leaf curl New Delhi virus (ToLCNDV) encodes the AC4 protein, which suppresses RNA silencing and aids in viral establishment (Vinutha *et al.*, 2018). AC4 specially interacts with the host AGO4 protein, but not AGO1, accumulating around the nucleus and affecting the methylation of the viral genome. This interaction inhibits the plant's RNA-directed DNA methylation pathway, thereby facilitating viral replication and persistence.

Despite successful RNA silencing responses against RNA viruses, DNA viruses like Tomato leaf curl virus (TLCV) have developed mechanisms to evade these defenses (Bian *et al.*, 2006). Transgenic tomato plants expressing TLCV *C2* or *C4* genes exhibited delayed viral infection and produced specific siRNAs, yet high levels of viral DNA persisted (Bian *et al.*, 2006). Methylation sequencing revealed extensive de novo methylation in viral DNA, suggesting that TLCV evades host defense by generating unmethylated viral DNA, thereby exploiting the host's methylation machinery to avoid silencing.

Tomato yellow leaf curl virus (TYLCV) employs the V2 protein to suppress transcriptional gene silencing (TGS) and deactivate host defense (Wang *et al.*, 2018b). V2 interacts with *Nicotiana benthamiana* histone deacetylase 6 (NbHDA6), which typically cooperates with

methyltransferase 1 (MET1) to facilitate gene silencing. While V2 does not inhibit HDA6's enzymatic activity, it competes with MET1 for binding to HDA6, reducing DNA methylation of the viral genome and increasing host susceptibility to TYLCV (Wang *et al.*, 2018b). LncRNAs are significant regulators in the tomato response to TYLCV infection (Wang *et al.*, 2015). RNA sequencing identified 1565 lncRNAs, including long intergenic ncRNAs and natural antisense transcripts. Several lncRNAs likely act as eTMs for miRNAs involved in the response to TYLCV, effectively modulating gene expression to enhance viral resistance (Wang *et al.*, 2015).

Research on tomato golden mosaic virus (TGMV) has demonstrated that DNA methylation significantly reduces viral DNA replication (Brough *et al.*, 1992). In experiments with *Nicotiana tabacum* protoplasts, cytosine residues were replaced with 5-methylcytosine, leading to lower viral DNA accumulation. This effect was observed regardless of whether methylation occurred on the viral or complementary strand. Interestingly, the methylation patterns introduced *in vitro* were not maintained in progeny viral DNA, indicating that maintenance methylation is not propagated in TGMV (Brough *et al.*, 1992).

Collectively, epigenetic mechanisms, particularly DNA methylation and lncRNAs, play crucial roles in tomato defense against viral infections. Understanding these processes provides valuable insights into plant-virus interactions and offers potential strategies for developing virus-resistant tomato cultivars.

### **Conclusions and future perspectives**

The comprehensive exploration of epigenetic mechanisms in tomato reveals their significant impact on abiotic and biotic stress responses. For instance, DNA methylation regulates gene expression in response to heat stress, chilling injury, and drought by modulating of stress-responsive genes. Histone modifications further contribute by altering chromatin structure and gene accessibility, which is crucial for timely stress responses. Additionally, non-coding RNAs, including miRNAs and lncRNAs, fine-tune gene expression and play essential roles in stress tolerance, as evidenced by their regulation of key genes involved in heat and drought stress responses. These insights underscore the potential of leveraging epigenetic modifications in breeding strategies. By understanding and manipulating these mechanisms, it is possible to develop tomato varieties that maintain high productivity and quality despite adverse

environmental conditions. This approach can be vital for ensuring food security in the face of climate change (Kakoulidou *et al.*, 2021; Sun *et al.*, 2021).

Further research is needed to better understand the underlying epigenetic mechanisms involved in tomato stress adaptation. A detailed mapping of the tomato epigenome under various stress conditions could facilitate the identification of key regulatory regions and epigenetic marks associated with stress tolerance (Gallusci *et al.*, 2017). This information could guide the development of targeted breeding programs. Additionally, integrating epigenomic data with traditional and molecular breeding techniques, such as marker-assisted selection and genomic selection, could accelerate the development of resilient tomato varieties. This integrated approach would optimize the selection of desirable traits and improve breeding efficiency.

Moreover, validating the role of specific DNA methyltransferases, histone modifiers, and non-coding RNAs in stress responses will provide deeper insights into their functions and potential applications in crop improvement. The development and application of advanced genome-editing tools, such as CRISPR/Cas9, for precise epigenetic modifications could enable the direct manipulation of stress-responsive genes and regulatory elements, enhancing stress tolerance in tomatoes (Pan *et al.*, 2021).

An important aspect of epigenetic is the heritability of linked traits. Investigating how environmental factors influence epigenetic modifications and how these changes are inherited across generations will offer valuable insights into the stability and heritability of epigenetic traits. Understanding these interactions could help predict plant responses to future climatic scenarios. Last but not least, comparative studies between tomato and other crops could uncover conserved epigenetic mechanisms, providing broader applications for epigenetic breeding strategies across different species.

In conclusion, advancing our understanding of epigenetic mechanisms in tomato stress adaptation offers significant potential for enhancing crop resilience and productivity. Integrating epigenetic insights into breeding programs can lead to the development of tomato varieties that thrive under the challenging conditions posed by climate change. This approach will contribute to global food security and promote sustainable agriculture.

### **Author contributions**

Sotirios Fragkostefanakis and Marianne Delarue designed the review, collected the references and wrote the manuscript and prepared the figure with the help of Moussa Benhamed. All authors contributed to and approved of the final manuscript.

### **Declaration of Competing Interest**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### **Acknowledgements**

The authors thank the reviewers for the valuable comments. SF acknowledges COST Action RECROP (CA22157) supported by the Cooperation in Science and Technology ([www.cost.eu](http://www.cost.eu)) for networking opportunities, and DFG support with the grant FR 3776/5-1.

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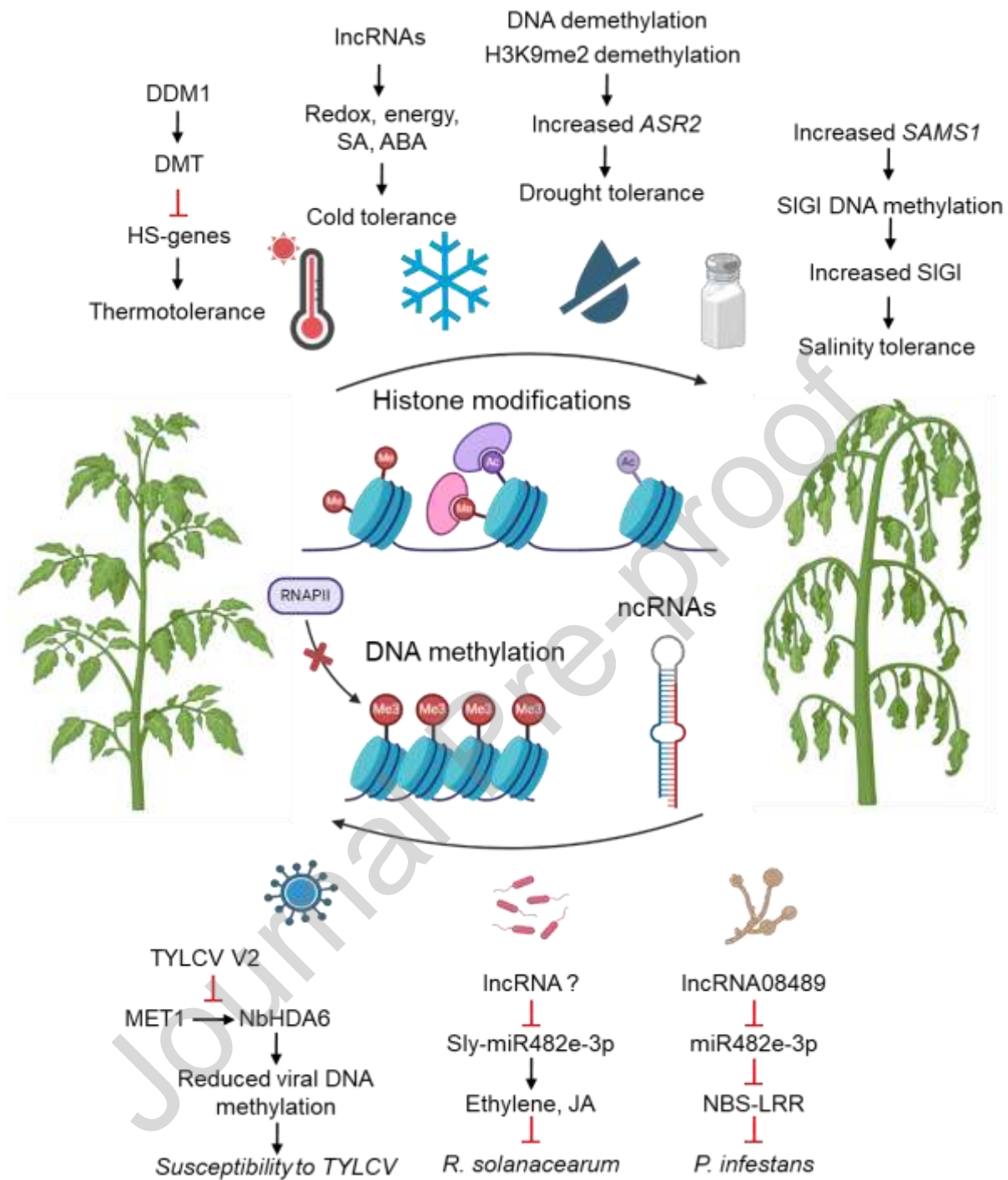
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**Figure 1. Examples of epigenetic mechanisms involved in abiotic and biotic stress resilience of tomato.** Details on the mechanisms are described in the text and in Tables 1 & 2. Part of the figure was designed with Biorender.

**Table 1. Overview of epigenetic mechanisms involved in tomato abiotic stress responses**

<b>Epigenetic Modification</b>	<b>Abiotic Stress</b>	<b>Epigenetic Changes</b>	<b>Mechanism</b>	<b>Reference</b>
DNA Methylation	Heat Stress	Methylation changes	Involves DDM1 enzyme allowing DNA methyltransferases to access heterochromatin, affecting gene expression and thermotolerance.	Singh et al., 2021; Iwasaki & Paszkowski, 2014
Histone Modification	Heat Stress	Histone acetylation	HSFB1 recruits HAC1 to chromatin, regulating gene expression for HS tolerance.	Bharti et al., 2004; Huang et al., 2023
Non-coding RNAs	Heat Stress	miR319d, miR169	miR319d and miR169 regulate gene expression to confer HS tolerance via HSF-mediated pathways.	Shi et al., 2019; Rao et al., 2020, 2022
DNA Methylation	Heat Stress	Methylation changes	Hot water treatment induces DNA methylation changes delaying postharvest ripening.	Pu et al., 2020
DNA Methylation	Chilling Injury	Methylation changes	Chilling increases DNA methylation of ripening-related gene promoters, reducing ethylene biosynthesis.	Zhang et al., 2016
Non-coding RNAs	Chilling Injury	lncRNAs	Differentially expressed lncRNAs target chilling stress-related proteins and enzymes.	Wang et al., 2018
RNA Modification	Chilling Injury	m6A methylation	m6A methylation affects RNA metabolism and response to chilling injury.	Bai et al., 2021; Yang et al., 2021
Histone Modification	Chilling Injury	H3K4me3 methylation	Coronatine treatment enhances H3K4me3 on CBF transcription factors, improving chilling resistance.	Liu et al., 2022a
Histone Modification	Drought Stress	H1 Histone Variant	Histone H1 variant accumulates under water-deficit conditions, influencing stress response.	Scippa et al., 2000; Kahn et al., 1993
DNA Methylation	Drought Stress	Demethylation	ASR2 gene demethylation correlates with drought-induced gene expression changes.	González et al., 2013
Histone Modification	Drought Stress	H3K9me2 demethylation	Mutations in SDG33/34 enhance drought tolerance by altering transcriptional context.	Bvindi et al., 2022

Non-coding RNAs	Drought Stress	lncRNAs, siRNAs	lncRNAs and siRNAs regulate gene expression for drought stress tolerance via RdDM pathway.	Lamin-Samu et al., 2021, 2022; Lu et al., 2024
Histone Modification	Salinity Stress	Histone acetylation	HDA1, HDA4, HDA9 regulate histone acetylation affecting gene expression under salt stress.	Guo et al., 2017; Yu et al., 2018
DNA Methylation	Salinity Stress	CHG-type methylation	SISAMS1 regulates DNA methylation of SIGI gene enhancing salt tolerance.	Chen et al., 2023
Non-coding RNAs	Salinity Stress	lncRNAs	lncRNAs in <i>S. pennellii</i> participate in stress response via hormone signaling pathways.	Guo et al., 2022
Histone Modification	Nutrient Deficiency	Histone methylation	Histone methyltransferases regulate N-responsive gene expression in an organ-specific manner.	Julian et al., 2023; Bvindi et al., 2022
DNA Methylation	Nutrient Deficiency	Hyper-/hypomethylation	Phosphate starvation alters DNA methylation affecting TE expression and Pi response genes.	Zeng et al., 2021
Non-coding RNAs	Nutrient Deficiency	miRNA168	miRNA168 targets AGO1, modulating small RNA pathways and enhancing potassium uptake.	Xian et al., 2014; Liu et al., 2020
Histone Modification	Heavy Metal Stress	Histone demethylation	Overexpression of SIJM524 increases Cd stress resistance by regulating metal transporter genes.	Li et al., 2022

**Table 2. Overview of epigenetic mechanisms involved in tomato biotic stress responses**

Epigenetic Modification	Biotic stress	Epigenetic Changes	Mechanism	Reference
Non-coding RNAs	Fungal diseases	lncRNAs	lncRNA08489 acts as a ceRNA for miR482e-3p, increasing NBS-LRR gene expression for resistance.	Liu et al., 2022a
Non-coding RNAs	Fungal diseases	lncRNAs	lncRNAs act as ceRNAs decoying miRNAs to regulate transcription factors and ROS levels.	Cui et al., 2020

Non-coding RNAs	Fungal diseases	lncRNAs	lncRNA16397 enhances glutaredoxin gene expression, reducing ROS during infection.	Cui et al., 2020
Non-coding RNAs	Fungal diseases	lncRNAs	SI-lncRNA47980 affects GA and phytohormone levels, altering plant immunity.	Su et al., 2023
Non-coding RNAs	Fungal diseases	miRNAs, lncRNAs	Silencing miR482e and overexpressing slncRNA39298 increases resistance to <i>P. infestans</i> .	Liu et al., 2022b
Non-coding RNAs	Fungal diseases	lncRNAs	SI-lncRNA20718 sequesters SI-miR6022, enhancing disease resistance by increasing PR genes.	Zhang et al., 2024
Non-coding RNAs	Fungal diseases	lncRNAs	lncRNA23468 reduces miR482b levels, increasing NBS-LRR gene expression for resistance.	Jiang et al., 2019
Histone Modification	Fungal diseases	H3K4me3, H3K9ac, H3K27me3	Changes in histone marks associated with gene responsiveness in response to <i>B. cinerea</i> .	Crespo-Salvador et al., 2018; Finiti et al., 2014
Non-coding RNAs	Fungal diseases	lncRNAs	lncRNA4504 involved in MeJA-induced resistance to <i>B. cinerea</i> in postharvest tomato.	Crespo-Salvador et al., 2018
Histone Modification	Fungal diseases	H2B ubiquitination	SIHUB1 and SIHUB2 regulate phenylpropanoid and SA-mediated pathways for resistance.	Zhang et al., 2015
Histone Modification	Fungal diseases	H3K36, H3K4 methylation	SDG33 and SDG34 alter histone methylations, increasing resistance to <i>B. cinerea</i> .	Bvindi et al., 2022a
Non-coding RNAs	Fungal diseases	lncRNAs	lncRNA MSTRG18363 decoys miR1918, enhancing expression of SIATL20 for resistance.	Zhou et al., 2021
Non-coding RNAs	Bacterial infections	lincRNAs	lincRNAs target genes related to JA and ethylene pathways in response to <i>R. solanacearum</i> .	Cao et al., 2022
Non-coding RNAs	Bacterial infections	lncRNAs, miRNAs	lncRNAs and miRNAs regulate receptor-like kinases and cell wall synthesis genes.	Si et al., 2023
RNA Silencing	Viral infections	Interaction with AGO4	ToLCNDV AC4 protein suppresses RNA silencing by interacting with AGO4, affecting methylation.	Vinutha et al., 2018



RNA Silencing	Viral infections	siRNAs	TLCV avoids silencing by generating unmethylated viral DNA.	Bian et al., 2006
Histone Modification	Viral infections	Interaction with HDA6	TYLCV V2 protein suppresses TGS by competing with MET1 for binding to HDA6.	Wang et al., 2018b
Non-coding RNAs	Viral infections	lncRNAs	lncRNAs act as eTMs for miRNAs, modulating gene expression to enhance viral resistance.	Wang et al., 2015
DNA Methylation	Viral infections	De novo methylation	DNA methylation reduces TGMV replication, but not maintained in progeny viral DNA.	Brough et al., 1992

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Highlights

- Histone modifications alter chromatin structure and gene accessibility, allowing timely stress response, and enhancing tomato's ability to cope with environmental challenges.
- miRNAs and lncRNAs fine-tune gene expression, playing essential roles in stress tolerance, particularly in heat and drought stress responses.
- Leveraging epigenetic modifications can develop tomato varieties that maintain high productivity and quality under adverse environmental conditions.
- Detailed mapping of the tomato epigenome under various stress conditions can identify key regulatory regions and guide targeted breeding programs