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Article

Histone deacetylase SlHDA7 impacts fruit ripening and shelf life in tomato

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Abstract

Fruit ripening depends on the accurate control of ripening-related genes expression, with histone deacetylases (HDACs) playing crucial roles in transcriptional regulation. However, the functions of HDACs in fruit maturation remain largely unexplored. Here, we show that SlHDA7 acts as a suppressor of fruit ripening and functions as an H4ac HDAC in tomato. Deletion of *SlHDA7* accelerated fruit ripening, while overexpression of *SlHDA7* delayed the maturation process. Additionally, ethylene production and carotenoid biosynthesis significantly increased in *slhda7* mutant fruits but decreased in *SlHDA7*-overexpressing fruits. Furthermore, SlHDA7 repress the expression of ethylene production and signaling, carotenoid metabolism, cell wall modification, and transcriptional regulation-related genes. RT-qPCR and ChIP-qPCR analyses indicated that SlHDA7 may deacetylate H4ac, leading to reduced transcript levels of *ACO1, GGPPS2*, *Z-ISO, EXP1*, and *XYL1* mRNA, consequently suppressing fruit ripening. Moreover, SlHDA7 suppresses fruit ripening by targeting specific ripening-associated transcription factors (TFs) like *RIN*, *FUL1*, and *ERF.E1*, ultimately leading to delayed ripening and prolonged fruit shelf life. In summary, our findings indicate that SlHDA7 negatively modulates tomato fruit maturation by adjusting H4ac levels of these ripening-associated genes and key TFs.

Introduction

Fleshy fruit ripening, essential for fruit quality, is a complex genetically coordinated process. Increasing evidence indicates that fruit ripening is controlled by intricate networks that integrate internal and external factors, leading to significant alters in color, flavor, texture, and other attributes [1]. In the case of climacteric fruits like tomato, ethylene plays a vital role in regulating fruit maturation [2]. Subsequent studies indicate that ethylene-mediated regulation of fruit ripening depends on the accurate management of the expression of numerous ripening-associated genes, which are precisely regulated at the epigenetic and transcriptional levels [3, 4].

Epigenetic modifications, such as DNA methylation, noncoding RNA, and histone modifications (methylation, acetylation, ubiquitination, phosphorylation, and so on), act as a crucial regulatory mechanism that controls chromatin status and gene transcription [5–7]. DNA methylation/demethylation is vital for fruit ripening [8–11]. Knocking out DNA demethylase (*SlDML2*) causes a non-ripening phenotype in tomato, indicating that SlDML2 plays a crucial role in regulating tomato fruit maturation [9, 12]. Notably, *SlDML2*-knockout fruits exhibit defective ethylene production, highlighting the importance of SlDML2 in ripening-induced ethylene biosynthesis [8, 12]. Alongside DNA methylation/demethylation, reversible methylation/demethylation of histones appears to be a critical mechanism for regulating ripening-associated gene expression and is essential for tomato fruit ripening [13, 14]. Despite the significant roles of epigenetic modifications in fruit maturation, the molecular regulation of these ripening-related genes by epigenetic modifications still requires further elucidation.

Histone acetylation, another conserved histone modification, plays vital roles in controlling chromatin structure and gene expression [15]. Histone deacetylases (HDACs) are highly conserved enzymes in eukaryotes and are responsible for removing acetyl groups from acetylated histones at lysine residues [15–17]. Over the past decade, HDACs have garnered significant attention and have been demonstrated to play crucial roles in the plant development process, including seed [18], vegetative development [19, 20], root epidermis [21, 22], flower development [23, 24], and leaf senescence [25], as well as stress responses [26]. In fruits, HDACs have been implicated as crucial regulators of fruit development and ripening [27–31]. For instance, CsHDC1 regulates cytokinin and polyamine biosynthesis and metabolism, and its downregulation results in a short-fruit phenotype [31]. MaHDA1 and CpHDA3 have been shown to suppress fruit ripening by directly interacting with the transcriptional repressors MaERF11 and CpERF9, respectively [27]. Similarly, MdHDA19 inhibits apple fruit ripening via interacting with MdERF4-MdTPL4 to

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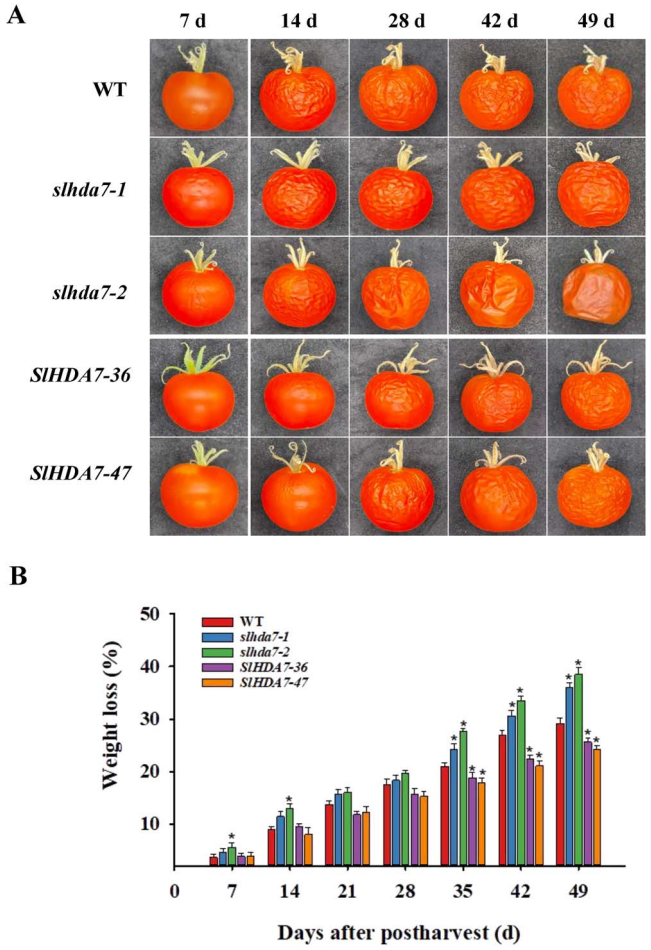


Figure 8. SlHDA7 extends the fruit shelf life of tomato. **A** Phenotypes of WT, *SlHDA7-OE*, and *slhda7* mutant fruits stored for 49 days. **B** The weight loss rate of WT, *SlHDA7-OE*, and *slhda7* mutant fruits during 49 days post-harvest storage. Data are means ± SD ($n = 3$). Asterisks indicate significant differences compared to WT by Student's *t* test (*$P < 0.05$).

were extracted and measured as previously described [59] and are expressed as $\mu g\ g^{-1}$ FW. The propectin and soluble pectin contents were measured as described previously [60]. Three biological replicates were conducted, with one replicate consisting of six fruits.

RT-qPCR assays

Total RNA of roots, stems, leaves, flowers, and tomato pericarp at 10, 20, 30, 36, 39, and 40 dpa was extracted with the HiPure Plant RNA Mini Kit (Magen, Guangzhou, China). First-strand cDNA was synthesized with a PrimeScript TM Reagent Kit (RR036A, Takara Bio Inc., Shiga, Japan) following the method described previously [56]. RT-qPCR was performed with an ABI7500 Real-Time PCR System (Thermo Fisher Scientific, Waltham, MA, USA) via using SYBR® Premix Ex TaqTM II (RR420A, TakaraBio Inc., Shiga, Japan). The gene expression level was calculated using the $2^{-\Delta\Delta Ct}$ method. The analysis included three independent biological replicates. *ACTIN* (Solyc03g078400) was chosen as the reference control.

RNA-seq assay

RNA was extracted from three independent WT and *slhda7* fruits at 36 dpa. The RNA extraction, library preparation, and Illumina sequencing were carried out at the Gene Denovo Company (Guangzhou, China) using the Illumina NovaSeq 6000 platform. The clean reads were compared with HISAT2 to the reference genome SL3.0. Gene expression levels were quantified using an RPKM value. Differentially expressed genes (DEGs) were identified based on the fold changes >2.5 with FDR <0.05 using DESEQ2. The gene functional enrichment analysis of the DEGs was conducted using the DAVID database (https://david.ncifcrf.gov/gene2gene.jsp).

Analysis of global histone acetylation

The levels of global histone acetylation in the leaves were assessed following previously established protocols [61]. Specific anti-acetylated histone antibodies were utilized for Western blot analysis. The quantification of immunoblotting signals was carried out using ImageJ. The specific anti-acetylated antibodies used in western blot assay were listed as: anti-H3 (ab1791; Abcam), anti-H3ac (17–615; Millipore), anti-H3K9ac (ab32129; Abcam), anti-H3K14ac (ab52946; Abcam), anti-H4 (ab177840; Abcam), and anti-H4ac (06–866; Millipore).

ChIP-qPCR analysis

ChIP-qPCR assays were conducted following the method described previously [13]. Fruits from the WT, *slhda7–1*, and SlHDA7–36 lines at 36 dpa were collected and promptly fixed with 1% formaldehyde under vacuum for 15 min, then quenched by adding glycine. After crosslinking, the chromatin complex was sonicated to approximately 500 bp fragments. Immunoprecipitation was carried out using an anti-acetyl-histone H4ac antibody (06–866; Millipore). The enrichment was assessed through qPCR and was normalized to the relative enrichment compared to the input. All primers utilized in ChIP-qPCR are listed in Table S1 (see online supplementary material).

Postharvest storage test

The fruits of the WT, *SlHDA7* overexpression lines, and *SlHDA7* knockout mutants were collected at the breaking stage and placed on a clean plate under greenhouse conditions for 16 hours during the day (25°C) and 8 hours during the night (22°C). The phenotype and fruit weight were monitored every 7 days. Each postharvest storage test utilized 20 fruits.

Statistical analysis

We used SPSS version 7.5 for statistical analysis. Variations among different sample groups were conducted with either Student's *t*-test or ANOVA.

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Author contributions

G.J. designed the experiments. Y.Z., Z.L., and H.H. performed the experiments. Y.Z. and G.J. wrote the paper. X.D., Y.J., X.S., and H.Q. edited the manuscript. All authors discussed and approved the final manuscript.

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Data availability

The RNA-Seq data have been deposited in the Dryad in the following repository (https://datadryad.org/stash/share/dFeS6NvPQK_xhouVJUpnPQYRN2R5VkjHNAvbqiel2R8).

Conflict of interests

The authors declare no competing interests.

Supplementary data

Supplementary data is available at *Horticulture Research* online.

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