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Expression of α -farnesene and ethylene biosynthesis genes in relation to superficial scald in 'White Winter Pearmain' apple during storage

Ruirui Ding^{1*} and Meiyang Wang^{1†}

Abstract

Superficial scald is a physiological disorder in apples (*Malus domestica*). A two-year study was performed to investigate the relationship between α -farnesene, ethylene, and superficial scald in 'White Winter Pearmain' apples. In the first year, untreated apples were stored at 0°C for 12 weeks in an observational experiment. Results indicated that the expression of ethylene perception genes and α -farnesene metabolism-related genes correlated with the onset of superficial scald. The second year involved an interventional study, where apples were treated with 1.25 mM lovastatin (LOV), 1.4 mM ethephon, and 700 mM 1-methylcyclopropene (1-MCP), prior to storage at 0°C for 12 weeks. After the storage, both LOV and 1-MCP significantly reduced α -farnesene, conjugated trienols (CTols), and ethylene levels, as well as the incidence of superficial scald, whereas flesh firmness was enhanced. The combination of LOV and 1-MCP showed the most pronounced effect, as justified by pronounced alterations in the relative expression levels of α -farnesene- and ethylene-related genes (α -farnesene synthase, *MdAFS*; 1-aminocyclopropane-1-carboxylate synthase 1, *MdACS1*; *MdACS4*; *MdACS5B*; 1-aminocyclopropane-1-carboxylate oxidase 1, *MdACO1*; *MdACO5*; *MdACO7*; ethylene receptor 5, *MdETR5*; *MdETR52*; and *MdETR102*) during storage. Correlation analysis showed a strong association between CTol content, ethylene production rate (EPR), and the expression of *MdAFS*, *MdACS4*, *MdACS5A*, *MdACS5B*, *MdACS7*, *MdACO1*, *MdACO5*, and *MdETR52* with superficial scald occurrence. These findings offer new insights into the molecular mechanisms by which α -farnesene and ethylene influence superficial scald development.

Keywords *Malus domestica*, α -Farnesene and conjugated trienols, Ethylene production rate, Superficial scald, LOV and 1-MCP, Gene expression

Introduction

Superficial scald is a physiological disorder marked by brown necrotic patches on the skin of apples (*Malus domestica*) (Larrigaudière et al. 2016; Whitaker 2013).

Varieties commonly susceptible to this disorder include 'Granny Smith' (Jemric et al. 2006; Pereira 2009; Watkins et al. 1995), 'Delicious' (Rupasinghe et al. 2000), 'Cortland' (Lu et al. 2013), 'Law Rome' (Alwan and Watkins 1999), 'Fuji' (Lu et al. 2011), 'Red Star' (Tong et al. 2002), and 'White Winter Pearmain' (Yuan et al. 2008). The characteristic brown spots on apple skins associated with superficial scald may lead to significant rot but do not affect the flesh (Chen et al. 2010; Gapper et al.

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2006). The development of superficial scald is linked to the accumulation of ethylene, α -farnesene, conjugated trienols (CTols), and reactive oxygen species (Karagianis et al. 2018; Sabbanamin et al. 2011; Whitaker 2007; Zhou et al. 2017).

The role of ethylene in fruit ripening is well-documented. 1-Methylcyclopropene (1-MCP), an ethylene inhibitor, acts as a competitive inhibitor of the 1-aminocyclopropane-1-carboxylate oxidase (ACO) enzyme, thereby inhibiting ethylene biosynthesis. This action reduces soft scald, core flush, and greasiness in apples (Balaguera-Lopez 2021; Fan and Mattheis 1999) while also suppressing superficial scald (Fan and Mattheis 1999; Jung and Watkins 2008; Yu and Yan 2017). 1-MCP decreases α -farnesene levels and the oxidation products of this compound, which are key in the development of superficial scald (Jung and Watkins 2008). In contrast, diphenylamine (DPA) prevents the oxidation of α -farnesene rather than its production. Isidoro and Almeida (2006) found that 1-MCP has a stronger inhibitory effect on the onset of superficial scald compared to DPA. Repeated 1-MCP treatments, especially within a few days post-harvest, yield the greatest benefits for fruit quality and scald control in faster-ripening cultivars like 'Cortland' (Lu et al. 2013), suggesting that the scald-suppressing and softening effects of 1-MCP are cultivar-dependent. However, additional factors such as exposure duration to 1-MCP, treatment temperature, and storage conditions also influence scald occurrence (DeEll et al. 2002; Xie et al. 2014). An untargeted metabolomic study on the effects of DPA and 1-MCP treatments on apple fruit suggested that terpene and phenolic compound metabolism may be implicated in scald development (Gong et al. 2021). Busatto et al. (2018) reported that 1-MCP inhibits the expression of polyphenol oxidase and upregulates enzymes involved in the metabolism of unsaturated long-chain fatty acids and sorbitol, which enhance tolerance to low temperatures. Ethylene synthesis and regulation are mediated by 1-aminocyclopropane-1-carboxylic acid synthase (ACS), ACO, and ethylene receptor (ETR) genes (Alexander and Grierson 2002; Ireland et al. 2012). Nineteen *MdACS* genes have been identified in apples, with *MdACS3a*, *MdACS5A*, *MdACS5B*, and *MdACS6–9* specifically expressed in fruits (Li et al. 2013). Seven *MdACO* genes have been identified (Clouse and Carraro 2014), of which *MdACO1–4* are expressed in fruits, with *MdACO1* playing a critical role in autocatalytic ethylene biosynthesis (Schaffer et al. 2007). ETRs are encoded by nine genes, including *MdETR1*, *MdETR1b*, *MdETR2*, *MdETR5*, *MdETRS1*, *MdETRS2*, *MdETR101*, *MdETR102*, and *MdETR105* (Ireland et al. 2012). It is well-established that these genes are primarily involved in fruit ripening and development at room temperature (Li et al. 2013; Yang et al. 2013, 2016). Although *MdACS1*,

MdACO1, and *MdERS1* are associated with ethylene synthesis during storage (Tsantili et al. 2007), the involvement of other genes in this process during cold storage in 'White Winter Pearmain' apples remains unclear.

During cold storage, α -farnesene synthesis predominantly occurs through the mevalonate (MVA) pathway in the apple cytoplasm (Rupasinghe et al. 2001). In this pathway, 3-hydroxy-3-methylglutaryl coenzyme A reductase (HMGR) catalyzes the conversion of 3-hydroxy-3-methylglutaryl coenzyme A (HMG-CoA) to MVA, a rate-limiting step in the production of isopentenyl pyrophosphate (Chye et al. 1992; Rupasinghe et al. 2001). The biosynthesis of α -farnesene is catalyzed by the α -farnesene synthase gene (*AFS*) (Pechous and Whitaker 2004; Yuan et al. 2008). Enzymes such as HMGR, mevalonate kinase (MVK), isopentenyl-diphosphate delta-isomerase (IPI), and farnesyl diphosphate synthase (FPPS) are potential regulators in the isoprenoid biosynthetic pathway (Liao et al. 2016). However, the relative expression levels of *MdHMGR*, *MdMVK*, *MdIPI*, *MdFPPS*, and *MdAFS* during storage, especially in response to lovastatin (LOV) and 1-MCP, remain underexplored. Three *MdHMGR* genes (*MdHMGR1–3*) and *MdAFS1* have been identified in apples (Lurie et al. 2005; Pechous and Whitaker 2002; Rupasinghe et al. 2001), but limited research has addressed *MdMVK*, *MdIPI*, and *MdFPPS*. LOV, a competitive HMGR inhibitor, has been shown to inhibit α -farnesene and scald (Ju and Curry 1999, 2000), and α -farnesene also serves as a cholesterol-lowering agent in humans at therapeutic doses (Alberts et al. 1980).

Both ethylene and α -farnesene-derived CTols are known to cause superficial scald, with LOV and 1-MCP significantly reducing its incidence. However, the gene expression changes underlying the effects of LOV and 1-MCP on α -farnesene and ethylene biosynthesis in relation to superficial scald have not been thoroughly investigated. In addition to the eight reported *HMGR* genes (*HMGR1–8*) in the apple genome, *MVK*, *IPI*, and *FPPS* genes were identified through NCBI (Ding et al. 2020). Moreover, the presence of additional ethylene synthesis-related genes, including those from the ACS, ACO, and ETR families, was confirmed. This study further examined the relationships between ethylene and α -farnesene synthesis genes and their expression during apple storage. Additionally, the effects of inhibitors of these pathways on the resistance of 'White Winter Pearmain' apples to superficial scald were explored, providing insights into the molecular mechanisms of these effects.

Materials and methods

Plant materials and treatments

'White Winter Pearmain' apples were harvested at commercial maturity in September 2023 and September 2024

from Valley Green Orchard in Tai'an City, Shandong Province, China. Selection criteria included uniform ripeness, absence of physical damage, and no treatments prior to postharvest. The first lot, consisting of 270 fruits, was stored at 0°C for 12 weeks. The second lot was stored at 0°C for 12 weeks (symptomatic period) with or without treatments. This lot was divided into seven sublots, each containing 210 fruits. The first subplot served as the control group (CK), with no treatment, and the second was treated with an LOV-free emulsion as a secondary control group (CK+emulsion). The third subplot was treated with a LOV emulsion at a concentration of 1.25mM, as described by Ju and Curry (2000). The fourth subplot was dipped in 1.4 mM ethephon (ETH) for 2 min. The fifth was exposed to 700 mM 1-MCP in a hermetically sealed chamber (28.75 m³) for 10 h. The sixth and seventh sublots received combinations of LOV, ETH, and 1-MCP as previously described, then stored at 0°C. The treatments included LOV, ETH, 1-MCP, LOV+ETH, LOV+1-MCP, CK, and CK+emulsion. After 12 weeks of storage (symptomatic period), the apples were transferred to 22°C to simulate shelf life for 7 d. Peel samples from ten fruits per treatment group were collected at two time points (12 weeks and 12 weeks+7 d), cut into small pieces, snap-frozen in liquid nitrogen, and stored at -80°C for further analysis.

Analyses of flesh firmness (FF) and soluble solid content (SSC)

FF in the equatorial region was measured using a GY-3 pressure tester (Zhejiang City Top Instrument, Zhejiang, China) with an 11 mm diameter probe. The SSC of freshly pressed juice samples was measured using a TD-45 digital refractometer (Zhejiang City Top Instrument, Zhejiang, China), following previously outlined procedures (Ding et al. 2019).

Evaluation of scald and determination of the ethylene production rate

For each treatment group, superficial scald incidence was visually assessed on 50 fruits after 12 weeks of storage at 0°C and 7 d at 22°C, with three replicates. Scald incidence was calculated as the percentage of fruits exhibiting skin lesions ≥ 1 cm², as described by Ding et al. (2019) and Xie et al. (2016).

Ethylene production rate (EPR) was measured using nine fruits per treatment group. Three fruits were sealed in a 3.8 L gas-tight jar and stored at 22°C for 1 h, with three replicates. Afterward, headspace gas was collected using a 1 mL gas-tight syringe *via* the septum on the jar lid and injected into a SPH-300A gas chromatograph (Beijing BCHP Analytical Technology Institute,

Beijing, China). Instrumentation conditions and calibration followed an external ethylene reference standard, as described by Ding et al. (2019).

Measurements of α -farnesene and CTols

A peel sample was placed in 6 mL of hexane in a 10 mL glass vial and incubated at 22°C for 20 min, with three replicates. After incubation, the samples were centrifuged at 13,000 $\times g$ for 5 min. Absorbance was measured at 232 nm and 281–290 nm using a UV-VIS spectrophotometer (UV-550, Shanghai Metash Instruments, Shanghai, China). The contents of α -farnesene and CTols were calculated based on molar extinction coefficients, $\epsilon_{232\text{ nm}}=27,740$ for α -farnesene and $\epsilon_{281-290\text{ nm}}=25,000$ for CTols, and expressed as g kg⁻¹ according to the data provided by Ding et al. (2019).

Quantitative reverse transcription–polymerase chain reaction (qRT–PCR) analysis

Total RNA from apple peel cDNA was reverse transcribed to generate first-strand cDNA using a first-strand cDNA synthesis kit. qRT–PCR was performed on a CFX96 Touch qRT–PCR machine (Bio-Rad, USA) using SYBR Real Master Mix (Bustin et al. 2009, 2010). The reaction conditions were as follows: 95°C for 30 s; 39 cycles of 5 s denaturation at 95°C, followed by 15 s of annealing and extension at 60°C; and 72°C for 20 s. Primer sequences, gene IDs, and accession numbers are listed in Supplementary Table S1. Three biological replicates were used for each gene analysis.

Statistical analysis

Experimental data were processed using Microsoft Excel 2019. All results are expressed as means $\pm$ SDs from at least three replicates. Statistical significance was assessed using Tukey's honestly significant difference ($P < 0.05$) test. Data analysis, column chart creation, and correlation analysis were conducted using SigmaPlot (version 12.0) and SPSS (version 16.0).

Results

Superficial scald, EPR, and expression of ethylene-related genes during storage

No scald symptoms were observed after 8 weeks of storage, while 8.2% of the fruits developed scald symptoms after 12 weeks (Fig. 1e). The EPR increased progressively throughout the 12-week cold storage period. Ethylene was undetectable in the peel tissues of 'White Winter Pearmain' apples at harvest. After 4 weeks of storage, the EPR rose to 1.5 $\mu\text{g kg}^{-1} \text{ h}^{-1}$ and peaked at 12 weeks (Fig. 1d).

Genes from the *MdACS*, *MdACO*, and *MdETR* families have been previously identified; however, those involved

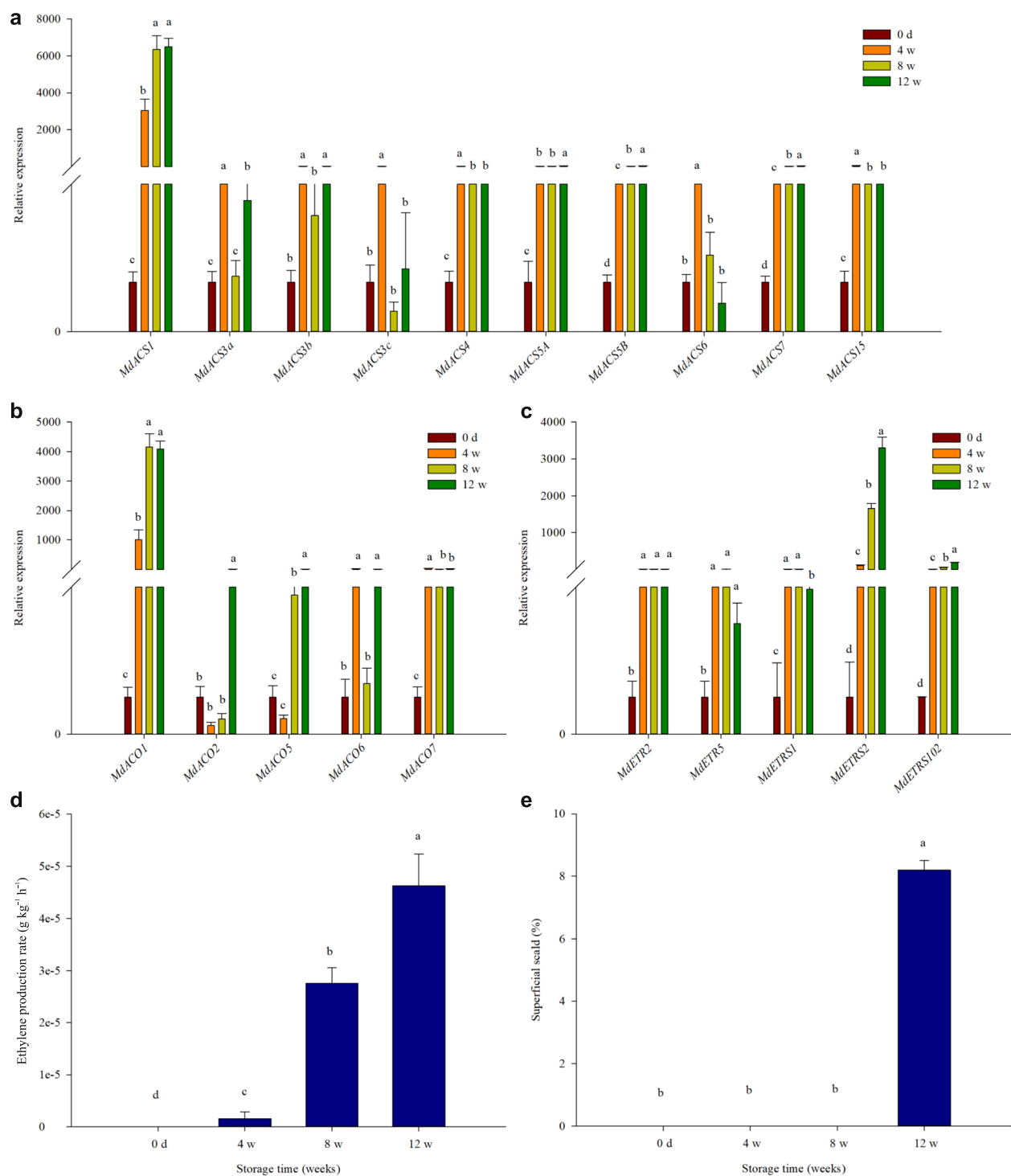


Fig. 1 Expression levels of 1-aminocyclopropane-1-carboxylate synthase 1 (ACS), 1-aminocyclopropane-1-carboxylate oxidase 1 (ACO), and ethylene receptor (ETR) family genes, ethylene production rate, and superficial scald incidence in 'White Winter Pearmain' apples (*Malus domestica*) during 12 weeks of storage at 0°C. **a–c** Expression levels of ACS (**a**), ACO (**b**), and ETR (**c**) family genes. **d** Ethylene production rate (EPR). **e** Incidence of superficial scald. Data are the means ± SD of three replicates. Different letters indicate significant differences ($P < 0.05$)

in the response to low temperature during the storage of ‘White Winter Pearmain’ apples remain uncharacterized. In this study, 19 *MdACS*, 7 *MdACO*, and 8 *MdETR* genes were identified, and their relative expression levels were measured during prolonged cold storage. Twenty genes—*MdACS1*, *MdACS3a*, *MdACS3b*, *MdACS3c*, *MdACS4*, *MdACS5A*, *MdACS5B*, *MdACS6*, *MdACS7*, *MdACS15*, *MdACO1*, *MdACO2*, *MdACO5–7*, *MdETR2*, *MdETR5*, *MdETR51*, *MdETR52*, and *MdETR102*—were expressed during storage (Fig. 1a–c). The incidence of superficial scald peaked at 12 weeks (Fig. 1e), coinciding with the peak relative expression of key ethylene synthesis genes (*MdACS1*, *MdACO1*, and *MdETR52*) (Fig. 1a). This suggests that upregulation of these genes plays a pivotal role in driving scald development during the later stages of storage. In contrast, the relative expression levels of other genes remained low throughout the storage period (Table 1).

Contents of α -farnesene and CTols and expression of α -farnesene synthesis-related genes

The α -farnesene content in apple peels increased gradually during the first 8 weeks of storage, followed by a decrease over the subsequent 4 weeks (Fig. 2b). The maximum α -farnesene content of 0.27 g kg⁻¹ was reached at 8 weeks. In contrast, the CTol content increased steadily from 0 to 0.043 g kg⁻¹ during the first 4 weeks of storage, with a significant rise after 8 weeks (Fig. 2c).

Although α -farnesene biosynthesis-related genes in apple cultivars have been reported and are available on the NCBI website, those involved in the response to low temperature during storage of ‘White Winter Pearmain’ apples remain uninvestigated. Expression analysis of eight members of the HMGR family (*MdHMGR1–8*), along with other related genes such as *MdMVK*, *MdIPI*, *MdFPPS*, and *MdAFS*, was conducted during fruit storage. Six genes—*MdHMGR1–3*, *MdHMGR5*, *MdMVK*, and *MdAFS*—were expressed during storage in ‘White Winter Pearmain’ apples (Fig. 2a). The relative expression levels of *MdHMGR1–3*, as well as *MdAFS*, were strongly correlated with α -farnesene content. Moreover, α -farnesene-derived CTols reached their peak at 12 weeks (Fig. 2c), indicating that the upregulation of these genes likely contributed to the synthesis of α -farnesene and CTols during the later storage period. In contrast, the relative expression levels of *MdHMGR4*, *MdHMGR6*, *MdHMGR7*, *MdHMGR8*, *MdIPI*, and *MdFPPS* remained low throughout storage (Table 1).

Effects of inhibitors on FF and SSC

The FF of ‘White Winter Pearmain’ apples decreased from 12.1 N (± 1.1 N) at commercial harvest to 10.0 N (± 1.8 N) during the late storage period, with these values serving as key maturity indices and commercial quality benchmarks, respectively. In the CK and CK+emulsion

groups, FF decreased from 9.9 and 10.2 N to 9.0 and 8.9 N, respectively, after 7 d of storage. Similar trends were observed in the LOV, ETH, 1-MCP, LOV+ETH, and LOV+1-MCP groups. FF was higher in all treatment groups compared to the CK and CK+emulsion groups after 12 weeks of storage at 0°C and 7 d at 22°C (Fig. 3a). No significant effects on SSC were observed in any treatment, with SSCs being comparable across all control and treatment groups (Fig. 3b).

Effect of inhibitors on superficial scald, ethylene production, α -farnesene, and CTol synthesis

After 12 weeks of storage, superficial scald was observed in the CK, CK+emulsion, and ETH groups. Scald incidences in these groups were 10.5%, 9.5%, and 18.2%, respectively, at 12 weeks, which increased to 13.3%, 17.6%, and 55.6%, respectively, after 7 d of storage. No scald was detected in the LOV, 1-MCP, LOV+ETH, and LOV+1-MCP groups after either 12 weeks of storage or 7 d at 22°C (Fig. 4a, b). These results indicate that both LOV and 1-MCP effectively prevent superficial scald development. Notably, no scald occurred even when ETH and LOV were co-applied.

Ethylene production remained high in the CK, CK+emulsion, ETH, and LOV+ETH groups after 12 weeks of storage, with no significant differences in ethylene release among these groups. However, after 7 d of storage, ethylene release from the CK and CK+emulsion groups increased slightly, whereas it significantly decreased in the LOV, 1-MCP, and LOV+1-MCP groups. The LOV+1-MCP treatment exhibited the most substantial inhibitory effect (Fig. 4c). These results suggest that both LOV and 1-MCP inhibit ethylene synthesis, with LOV's suppression being counteracted by exogenous ETH application.

No significant differences in α -farnesene content were observed between the CK, CK+emulsion, LOV, and ETH groups, with α -farnesene levels remaining stable after both 12 weeks of storage and 7 d of storage. However, α -farnesene content was lower in the 1-MCP, LOV+ETH, and LOV+1-MCP groups compared to the CK and CK+emulsion groups after both storage periods. Notably, LOV+1-MCP significantly inhibited α -farnesene synthesis more effectively than 1-MCP or LOV+ETH alone after 7 d of storage (Fig. 4d).

In contrast to the CK and CK+emulsion groups, the ETH group showed no change in CTol content after 12 weeks of storage and 7 d at 22°C. Treatments with LOV, 1-MCP, LOV+ETH, and LOV+1-MCP all inhibited CTol production, with LOV+1-MCP proving the most effective in this regard (Fig. 4e). These results indicate that the combination of LOV and 1-MCP has a more potent inhibitory effect on both α -farnesene and CTol synthesis than either compound individually.

Table 1 List of different genes expressed in apple fruit during 12 weeks of storage at 0°C

Gene name	Fold change (0d/0d)	Fold change (4w/0d)	Fold change (8w/0d)	Fold change (12w/0d)
<i>MdACO1**</i>	1.00 ± 0.27	1011.89 ± 331.11	4155.81 ± 447.97	4085.86 ± 271.47
<i>MdACO2*</i>	1.00 ± 0.28	0.23 ± 0.07	0.41 ± 0.14	14.20 ± 2.63
<i>MdACO3</i>	1.00 ± 0.34	0.01 ± 0.06	0.02 ± 0.01	0.15 ± 0.11
<i>MdACO4</i>	1.00 ± 0.30	0.34 ± 0.13	1.49 ± 0.88	3.20 ± 1.67
<i>MdACOS*</i>	1.00 ± 0.31	0.42 ± 0.09	3.77 ± 0.35	7.22 ± 1.19
<i>MdACO6*</i>	1.00 ± 0.49	14.94 ± 5.07	1.37 ± 0.42	9.27 ± 2.86
<i>MdACO7*</i>	1.00 ± 0.28	36.15 ± 7.67	13.52 ± 1.83	15.06 ± 3.52
<i>MdACS1**</i>	1.00 ± 0.21	3047.07 ± 612.53	6359.44 ± 733.08	6506.82 ± 438.32
<i>MdACS3a*</i>	1.00 ± 0.22	5.06 ± 0.70	1.12 ± 0.32	2.66 ± 1.65
<i>MdACS3b*</i>	1.00 ± 0.24	10.86 ± 2.74	2.36 ± 0.68	8.91 ± 2.67
<i>MdACS3c*</i>	1.00 ± 0.35	11.16 ± 1.65	0.40 ± 0.18	1.27 ± 1.14
<i>MdACS4*</i>	1.00 ± 0.22	8.85 ± 1.71	3.90 ± 1.08	4.82 ± 2.13
<i>MdACS5A*</i>	1.00 ± 0.42	15.57 ± 1.54	16.70 ± 2.09	40.80 ± 2.08
<i>MdACS5B*</i>	1.00 ± 0.14	4.06 ± 0.81	10.15 ± 3.15	29.95 ± 3.46
<i>MdACS6*</i>	1.00 ± 0.15	5.15 ± 0.74	1.55 ± 0.46	0.57 ± 0.41
<i>MdACS7*</i>	1.00 ± 0.12	4.53 ± 0.48	12.18 ± 3.68	25.07 ± 3.97
<i>MdACS8</i>	1.00 ± 0.27	0.19 ± 0.02	0.50 ± 0.17	1.40 ± 0.78
<i>MdACS9</i>	1.00 ± 0.16	0.53 ± 0.08	2.29 ± 0.68	2.98 ± 1.67
<i>MdACS10</i>	1.00 ± 0.16	0.06 ± 0.01	0.28 ± 0.15	0.59 ± 0.57
<i>MdACS11</i>	1.00 ± 0.22	0.02 ± 0.01	1.07 ± 0.54	0.30 ± 0.18
<i>MdACS12</i>	1.00 ± 0.68	0.01 ± 0.00	0.18 ± 0.08	0.36 ± 0.24
<i>MdACS13</i>	1.00 ± 0.18	0.04 ± 0.01	0.22 ± 0.08	0.53 ± 0.29
<i>MdACS14</i>	1.00 ± 0.33	0.07 ± 0.02	0.25 ± 0.11	0.27 ± 0.15
<i>MdACS15*</i>	1.00 ± 0.22	45.44 ± 8.64	6.20 ± 2.08	3.66 ± 0.91
<i>MdACS16</i>	1.00 ± 0.16	0.68 ± 0.41	0.83 ± 0.55	0.28 ± 0.06
<i>MdACS17</i>	1.00 ± 0.62	0.15 ± 0.013	0.09 ± 0	0.21 ± 0.03
<i>MdETR1</i>	1.00 ± 0.43	1.14 ± 0.74	0.75 ± 0.39	1.15 ± 0.26
<i>MdETR1b</i>	1.00 ± 0.48	2.38 ± 1.66	2.67 ± 1.93	2.61 ± 1.81
<i>MdETR2*</i>	1.00 ± 0.43	6.95 ± 1.02	8.50 ± 1.71	9.81 ± 2.13
<i>MdETR5*</i>	1.00 ± 0.44	4.05 ± 0.48	4.44 ± 1.25	3.00 ± 0.56
<i>MdETR51*</i>	1.00 ± 0.93	9.75 ± 1.13	11.70 ± 1.21	3.94 ± 0.61
<i>MdETR52**</i>	1.00 ± 0.95	104.39 ± 17.93	1661.69 ± 129.63	3306.69 ± 283.74
<i>MdETR102**</i>	1.00 ± 0.09	10.29 ± 0.66	57.04 ± 4.00	183.83 ± 15.89
<i>MdETR105</i>	1.00 ± 0.01	1.30 ± 0.14	1.42 ± 0.51	0.28 ± 0.09
<i>MdHMGR1*</i>	1.00 ± 0.72	8.93 ± 0.71	29.56 ± 0.38	39.08 ± 0.68
<i>MdHMGR2*</i>	1.00 ± 0.83	11.14 ± 0.15	46.56 ± 0.03	57.68 ± 0.14
<i>MdHMGR3**</i>	1.00 ± 0.86	2.74 ± 0.17	197.85 ± 0.73	420.89 ± 0.74
<i>MdHMGR4</i>	1.00 ± 0.04	0.86 ± 0.59	2.05 ± 1.02	4.75 ± 0.94
<i>MdHMGR5*</i>	1.00 ± 0.68	3.79 ± 0.83	1.84 ± 0.15	16.19 ± 0.03
<i>MdHMGR6</i>	1.00 ± 0.43	1.38 ± 0.69	1.31 ± 0.65	3.25 ± 0.02
<i>MdHMGR7</i>	1.00 ± 0.50	0.55 ± 0.47	0.44 ± 0.26	2.36 ± 0.29
<i>MdHMGR8</i>	1.00 ± 0.40	0.60 ± 0.20	1.00 ± 0.83	0.79 ± 0.64
<i>MdMVK*</i>	1.00 ± 0.08	2.09 ± 0.66	2.61 ± 0.69	6.96 ± 0.52
<i>MdIPI</i>	1.00 ± 0.52	1.09 ± 0.63	0.98 ± 0.01	2.04 ± 0.20
<i>MdFPPS</i>	1.00 ± 0.16	3.33 ± 0.99	1.66 ± 0.70	3.63 ± 0.92
<i>MdAFS**</i>	1.00 ± 0.08	1310.32 ± 65.28	208.48 ± 31.45	163.36 ± 17.67

Fold changes are shown relative to the 0-day time point (set as 1). Values at 4, 8, and 12 weeks represent expression changes compared with the 0-day baseline.

Genes marked with asterisks were validated as significantly different by qRT-PCR. *MdACOs*, *Malus domestica* 1-aminocyclopropane-1-carboxylate oxidase; *MdACSs*, 1-aminocyclopropane-1-carboxylate synthase; *MdETRs*, ethylene receptors; *MdHMGs*, 3-hydroxy-3-methylglutaryl coenzyme A; *MdMVK*, mevalonate kinase; *MdIPI*, isopentenyl-diphosphate delta-isomerase; *MdFPPS*, farnesyl diphosphate synthase; *MdAFS*, α -farnesene synthase

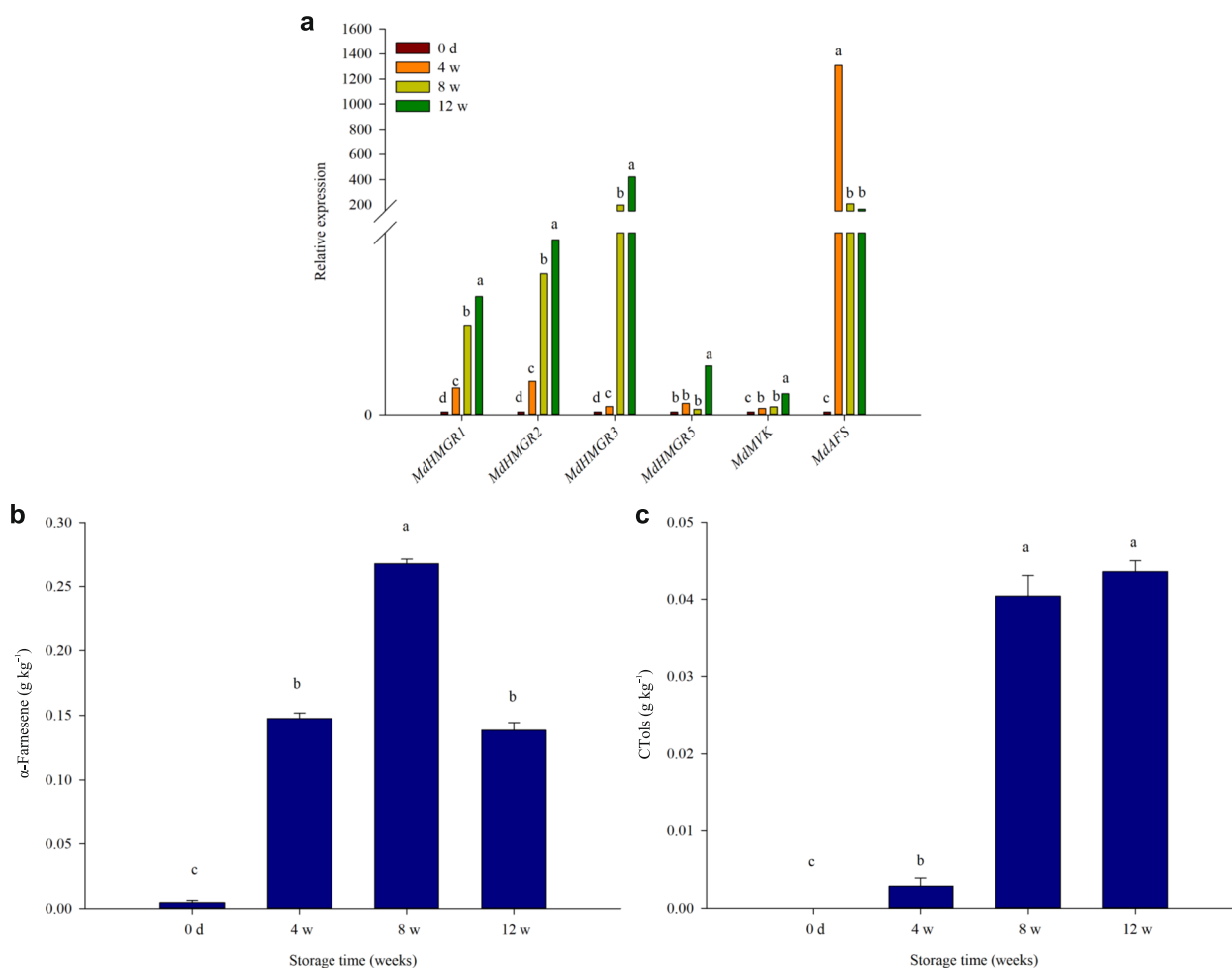


Fig. 2 Expression levels of α-farnesene synthesis-related genes, and α-farnesene and conjugated trienols (CTols) contents in 'White Winter Pearmain' apples (*Malus domestica*) during 12 weeks of storage at 0°C. **a** Expression of α-farnesene synthesis-related genes. HMGR, 3-hydroxy-3-methylglutaryl coenzyme A reductase. **b** α-Farnesene content. **c** CTols content. Data are the means ± SD of three replicates. Different letters indicate significant differences ($P < 0.05$)

Heatmap and correlation analyses revealed the effects of inhibitors on the relative expression levels of ethylene and α-farnesene biosynthesis genes

Hierarchical cluster analysis was performed to examine the impact of applied inhibitors on the expression of genes involved in ethylene synthesis, ETR, and α-farnesene biosynthesis. A total of 26 genes were quantified in 'White Winter Pearmain' apples (Table S2). Compared to the CK group after 12 weeks of storage, the other treatment groups showed significant reductions in the relative expression levels of 18 genes and increases in 4 genes after both 12 weeks of storage and 7 d at 22°C (Fig. 5).

Pearson's correlation analysis of the seven groups revealed significant correlations between superficial scald incidence, CTol content, and ethylene synthesis ($r_s = 0.793$ and 0.737 , respectively; $P < 0.05$) in apples after 12 weeks of cold storage (Table S3). The incidence of

superficial scald was strongly correlated with the production of α-farnesene and ethylene, based on the transcription levels of *MdAFS*, *MdACS4*, *MdACS5A*, *MdACS5B*, *MdACS7*, *MdACO1*, *MdACO5*, and *MdERTS2* ($r_s = 0.948$, 0.877 , 0.875 , 0.946 , 0.724 , 0.807 , 0.97 , and 0.722 , respectively; $P < 0.05$ and $P < 0.01$). In contrast, the incidence of superficial scald showed only weak correlations with α-farnesene production, FF, and SSC ($r_s = 0.653$, -0.721 , and 0.127 , respectively). These findings indicate that the accumulation of CTols and the key genes associated with α-farnesene and ethylene synthesis play a critical role in the development of scald after low-temperature storage.

Discussion

The development of superficial scald is linked to the production of ethylene and CTols, which result from the oxidation of α-farnesene during fruit storage (Zhou et al.

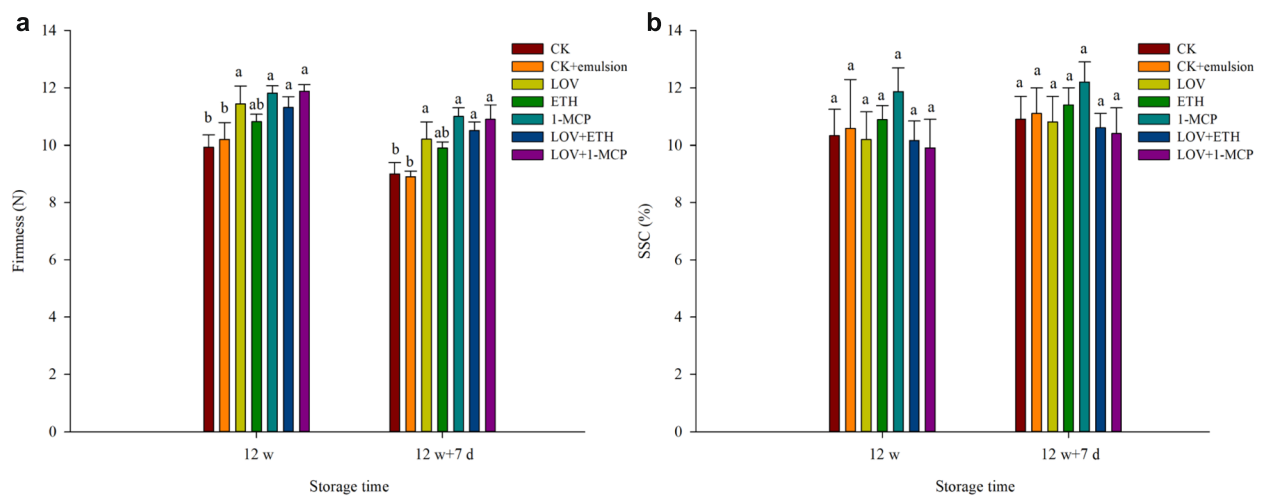


Fig. 3 Effects of lovastatin (LOV), ethephon (ETH), and 1-methylcyclopropene (1-MCP) on flesh firmness (FF) and soluble solid content (SSC) in 'White Winter Pearmain' apples during 12 weeks of storage at 0°C and subsequent 7 d of storage at 22°C. **a** Flesh firmness. **b** SSC content. Data are the means $\pm$ SD of three replicates. Different letters indicate significant differences ($P < 0.05$)

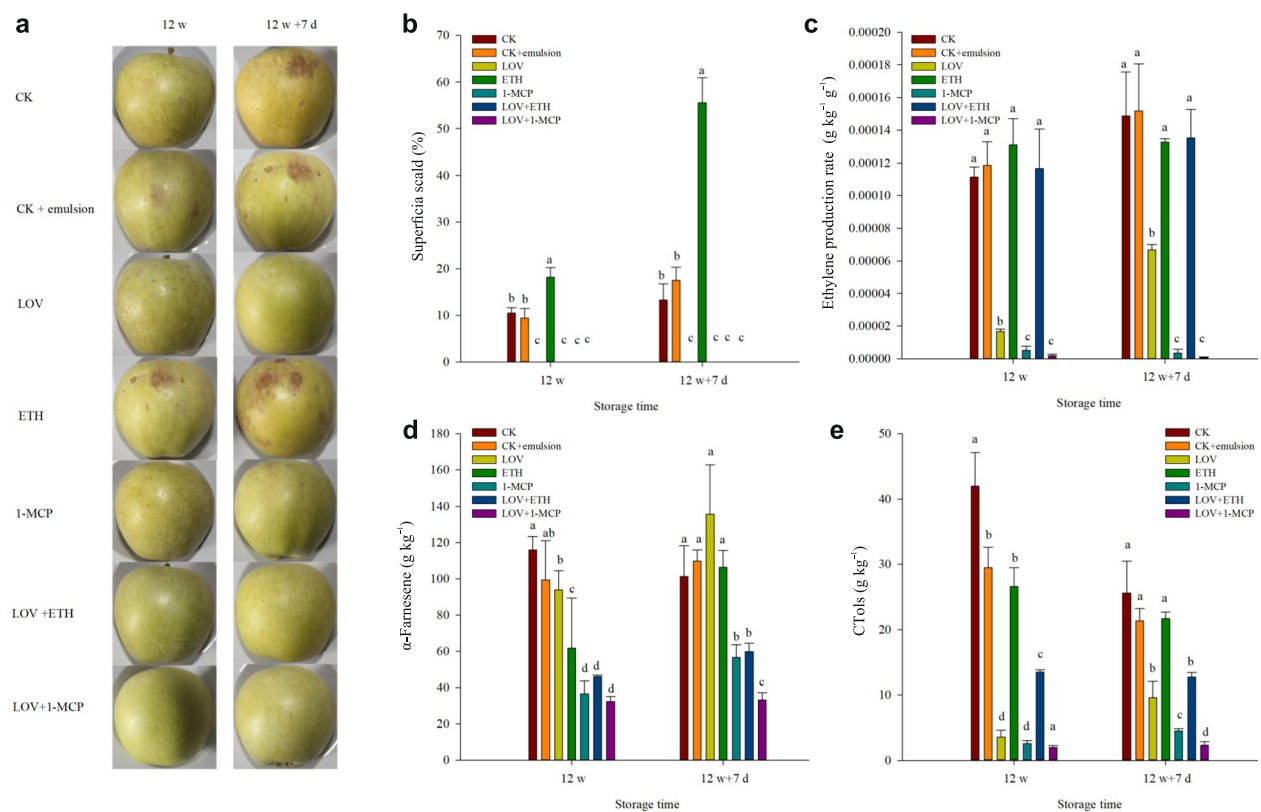


Fig. 4 Superficial scald incidence, ethylene production rate (EPR), and α-farnesene and conjugated trienols (CTols) contents in 'White Winter Pearmain' apples with lovastatin (LOV), ethephon (ETH), and 1-methylcyclopropene (1-MCP) treatment during 12 weeks of storage at 0°C, followed by 7 d of shelf-life simulation at 22°C. **a** Apple phenotype. **b** Superficial scald incidence. **c** Ethylene production rate. **d** α-Farnesene content. **e** CTol content. Data are the means $\pm$ SD of three replicates. Different letters indicate significant differences ($P < 0.05$)

2017). While most studies have focused on genes related to fruit development, maturation, ethylene synthesis, and signal transduction—such as those encoding ACS,

ACO, and ETR (Clouse and Carraro 2014; Ireland et al. 2012; Li et al. 2013)—the expression of these genes during fruit storage remains underexplored. In this study,

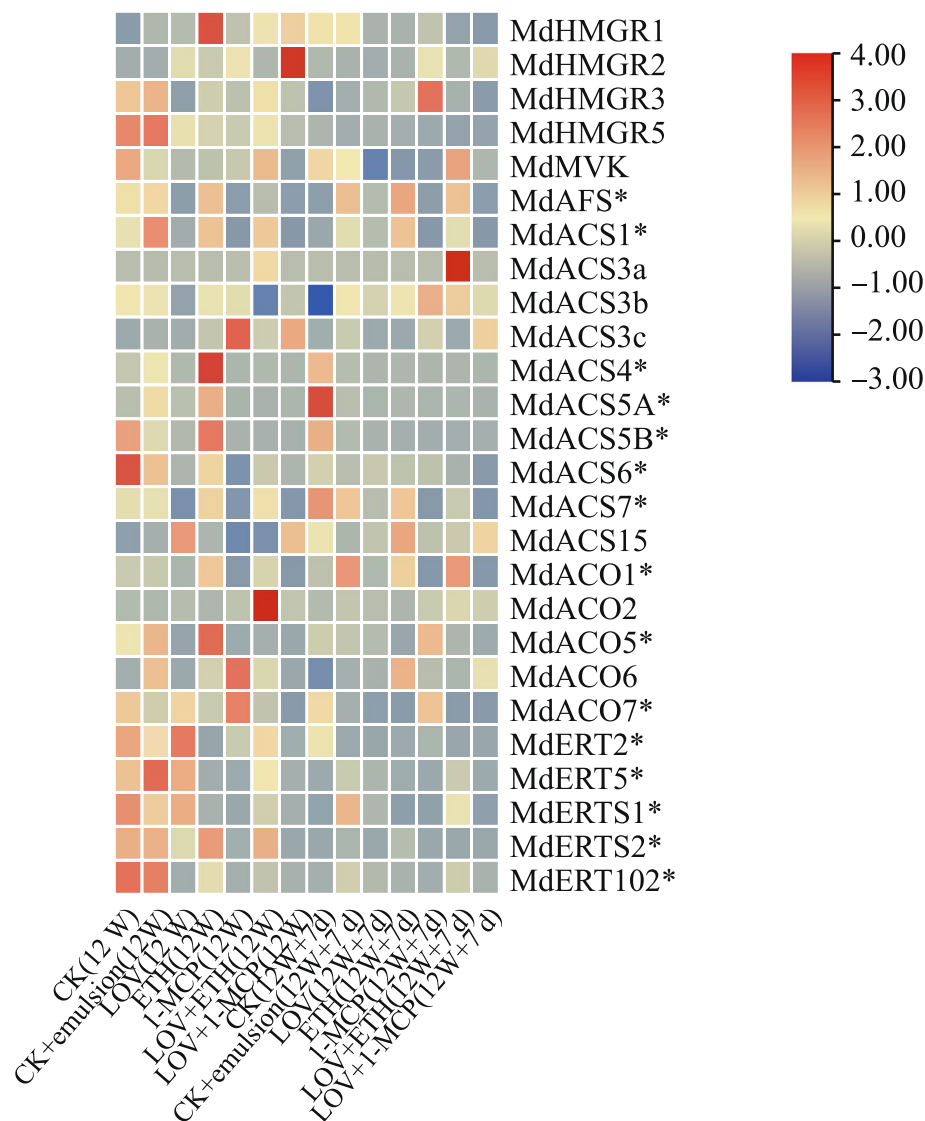


Fig. 5 Hierarchical cluster analysis of the expression levels of 1-aminocyclopropane-1-carboxylate synthase 1 (ACS), 1-aminocyclopropane-1-carboxylate oxidase 1 (ACO), and ethylene receptor (ETR), and α -farnesene metabolism-related genes under lovastatin (LOV), ethephon (ETH), and 1-methylcyclopropene (1-MCP) treatment during 12 weeks of storage at 0°C plus 7 d of storage at 22°C in ‘White Winter Pearmain’ apples. CK, control group. Data are the means $\pm$ SD of three replicates. Different letters indicate significant differences ($P < 0.05$). * indicates important genes

20 genes from the *MdACS* (1, 3a, 3b, 3c, 4, 5A, 5B, 6, 7, and 15), *MdACO* (1, 2, 5, 6, and 7), and *MdETR* (2, 5, S1, S2, and 102) families were found to be expressed during the storage of ‘White Winter Pearmain’ apples. A previous study indicated that only *MdACS1*, *MdACO1*, and *MdETR1* are involved in ethylene release during fruit storage (Tsantili et al. 2007). However, our results provide comprehensive evidence that the expression of these genes is significantly upregulated during storage. *MdAFS1* is the most extensively studied gene related to α -farnesene synthesis (Pechous and Whitaker 2004; Yuan et al. 2008). However, the relative expression of its

precursor substrate genes and upstream synthase genes has not been well explored. Our findings showed that CTol content gradually increased during storage, while α -farnesene content reached its maximum at 8 weeks. The relative expression levels of six genes—*MdHMGR1*–3, *MdHMGR5*, *MdMVK*, and *MdAFS*—were also elevated during storage. These results suggest that α -farnesene, CTol, and ethylene synthesis are induced by low temperature, with most of the α -farnesene and ethylene synthesis-related genes, including *MdAFS*, *MdACS1*, *MdACS4*, *MdACS5B*, *MdACO1*, *MdACO5*, *MdACO7*, *MdETR5*, *MdETR2*, and *MdETR102*, being closely

associated with low-temperature conditions. Notably, the expression of *MdAFS*, *MdACS1*, *MdACO1*, and *MdETR2* was particularly upregulated.

1-MCP is an ethylene perception inhibitor (Varanasi et al. 2013), while LOV significantly inhibits α -farnesene synthesis (Ju and Curry 1999, 2000). However, limited research has investigated the effects of ethylene and α -farnesene synthesis inhibitors, particularly transcription inhibitors, on superficial scald development. Our results suggest that both 1-MCP and LOV significantly reduce ethylene and CTol levels, effectively inhibiting scald occurrence. However, LOV did not reduce α -farnesene release during the symptomatic period. Some studies have shown that LOV possesses inherent antioxidant activity (Ailed et al. 2023; Tan et al. 2017), which may explain its role as a free radical scavenger, preventing α -farnesene oxidation. Thus, beyond inhibiting HMGR, LOV may directly impede the conversion of α -farnesene to CTols *via* its antioxidant properties. Interestingly, the incidence of superficial scald increased in the ETH group, while no scald was observed in the LOV+ETH group. This suggests that LOV's ability to block α -farnesene oxidation may be a key factor in preventing scald development. Furthermore, the LOV+1-MCP treatment proved more effective in reducing ethylene, α -farnesene, and CTol levels, as well as scald incidence. Both LOV and 1-MCP also increased FF but had minimal impact on SSC, indicating that these treatments improve fruit quality. Our results demonstrate that 1-MCP inhibits ethylene release, while LOV inhibits CTol synthesis rather than α -farnesene production. Despite acting on distinct steps, the combined inhibitory effects of 1-MCP and LOV likely lead to broader metabolic changes in the fruit. This study provides new insights into the mechanisms underlying scald occurrence.

The relationship between genes associated with ethylene and α -farnesene synthesis and superficial scald was also explored. Genes involved in ethylene biosynthesis and receptor activity have been extensively studied in apples (Eisenreich et al. 2001; Golding et al. 2001; Ireland et al. 2012). In our study, high ethylene production in 'White Winter Pearmain' apples after storage coincided with increased expression of *MdACS1*, *MdACS4*, *MdACS5A*, *MdACS5B*, *MdACS6*, *MdACS7*, *MdACO1*, *MdACO5*, *MdACO7*, *MdETR2*, *MdETR5*, *MdETR51*, *MdETR52*, and *MdETR102*. In contrast, the LOV and 1-MCP groups exhibited a reduction in the expression of these genes. Most of these genes, including *MdACS1*, *MdACS3*, *MdACS3a*, and *MdACS6–9*, *MdACO1*, *MdACO2*, and *MdACO3*, *MdETR1*, *MdETR2*, and *MdETR5* (Yang et al. 2013), are associated with ethylene biosynthesis. The expression of *MdACS1*, *MdACS4*, *MdACS5B*, *MdACO1*, *MdACO5*, *MdACO7*, *MdETR5*,

MdETR52, and *MdETR102* was significantly inhibited by LOV and 1-MCP during storage. Correlation analysis confirmed a strong association between EPR and key genes involved in ethylene synthesis, with scald severity. These results indicate that ethylene biosynthesis-related genes play pivotal roles during fruit storage and that LOV and 1-MCP treatments modulate the expression of these genes, reducing the severity of scald.

In plant tissues, α -farnesene biosynthesis primarily occurs through the cytoplasmic MVA pathway (Xie et al. 2014). Two *HMGR* genes are differentially expressed during apple development, with *MdHMGR2* transcription levels increasing during fruit storage (Rupasinghe et al. 2001). Notably, *MdHMGR2* expression significantly increased, while *MdHMGR3* expression modestly rose in 1-MCP-treated 'Granny Smith' apples (Lurie et al. 2005). The current study found that the expression of *MdHMGR1–3* and *MdHMGR5* is induced by cold storage. Additionally, the expression of *MdHMGR3* and *MdHMGR5* remained low in all inhibitor-treated groups. α -Farnesene synthesis *via* the cytoplasmic MVA pathway is regulated by *AFS* in plant tissues (Pechous and Whitaker 2004). These findings suggest that LOV and 1-MCP may support long-term cold storage of fruit by inhibiting the expression of α -farnesene synthesis genes such as *MdHMGR3*, *MdHMGR5*, and *MdAFS*. However, the expression of *MdHMGR1*, *MdHMGR2*, and *MdMVK* either increased or remained unchanged after treatment with LOV and 1-MCP. While the correlation between α -farnesene content and the incidence of superficial scald was weak, scald formation showed a strong association with CTol levels and key genes involved in α -farnesene synthesis. These results highlight the importance of α -farnesene biosynthesis-related genes in fruit storage, providing a molecular foundation for scald development. Future research will focus on validating gene function through transient or stable expression in apple fruit or callus tissues to further elucidate the roles of specific candidate genes in scald occurrence.

Conclusions

In conclusion, the levels of CTols and ethylene production are closely associated with the incidence of superficial scald during storage. Most genes involved in α -farnesene and ethylene synthesis are upregulated by low temperatures. Fruits treated with LOV and 1-MCP show no scald and exhibit significant reductions in α -farnesene, CTol, and ethylene synthesis during long-term storage. In contrast, ETH-treated fruits develop severe scald. In this study, LOV and 1-MCP significantly inhibited the transcription of *MdAFS*, *MdACS1*, *MdACS4*, *MdACS5B*, *MdACO1*, *MdACO5*, *MdACO7*, *MdETR5*, *MdETR52*, and *MdETR102* at later stages of

storage. These findings suggest that LOV and 1-MCP improve apple storability by downregulating the expression of genes related to α -farnesene and ethylene synthesis, thereby reducing the incidence of superficial scald. Further investigation of gene expression during scald development will facilitate the design of effective strategies to mitigate superficial scald in stored fruit, while also enhancing our understanding of the role of α -farnesene and ethylene synthesis genes during fruit storage.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1007/s44281-026-00100-2>.

Supplementary Material 1: Table S1. Primers for the quantitative qRT-PCR analysis, gene name, and GenBank accession number. Both forward and reverse primers are shown. *MdACOs*, *Malus domestica* 1-aminocyclopropane-1-carboxylate oxidase; *MdACSs*, 1-aminocyclopropane-1-carboxylate synthase; *MdETRs*, ethylene receptors; *MdHMGRs*, 3-hydroxy-3-methylglutaryl coenzyme A reductase; *MdMVK*, mevalonate kinase; *MdIPI*, isopentenyl-diphosphate delta-isomerase; *MdFPPS*, farnesyl diphosphate synthase; *MdAFS*, α -farnesene synthase. Table S2. The identified genes and their quantitative changes during 12 weeks of storage at 0°C plus 7 d of storage at 22°C in 'White Winter Pearmain' apple. Table S3. Pearson correlation coefficients between superficial scald and firmness, soluble solid content (SSC), ethylene production rate (EPR), α -farnesene, conjugated trienols (CTols), and the transcription levels of α -farnesene and ethylene biosynthesis-associated genes in 'White Winter Pearmain' apples after 12 weeks of cold storage.

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Authors' contributions

RRD conceived, designed, and performed the experiments. RRD and MYW analyzed the data and drafted the manuscript. RRD formatted the figures, and revised the manuscript. All authors have read and approved the final manuscript.

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Data availability

Date will be shared upon request by the readers.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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