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Cut-Wounding Promotes Phenolic Accumulation in *Cucumis melo* L. Fruit (cv. Yugu) by Regulating Sucrose Metabolism

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Abstract: The effect of cutting on the molecular changes underlying sucrose metabolism and the phenylpropanoid pathway in melon fruit (cv. Yugu) during storage at 15 °C was investigated. Furthermore, the key metabolites, enzymes, and genes involved in sucrose and phenylpropanoid metabolism were determined. Results showed that the cutting of melon increased the activities of acid invertase (AI), neutral invertase (NI), and sucrose synthase-cleavage (SS-c) and the expressions of *CmAI1/2*, *CmNI1/2*, and *CmSS1*, while sucrose synthase-synthesis (SS-s) and sucrose phosphate synthase (SPS) activities and the *CmSS2/3* and *CmSPS1/2/4* gene expressions were suppressed. These led to sucrose decomposition and fructose and glucose accumulation in fresh-cut melon at the early stage of storage. Moreover, cutting increased the activity and gene expression of hexokinase, which accelerated the transformation of hexose in fresh-cut melon. In addition, cutting enhanced the activities of phenylalanine ammonia lyase (PAL), cinnamate-4-hydroxylase (C4H), and 4-coumarate-CoA ligase (4CL) and up-regulated the expressions of *CmPAL1-9*, *CmC4H1-4*, and *Cm4CL1/2/3*, which activated phenylpropanoid metabolism and resulted in phenolic accumulation in fresh-cut melon. These findings demonstrate that cutting of melon can enhance sucrose metabolism and phenylpropanoid pathway by regulating the activities and gene expressions of related enzymes. Therefore, cut-wounding promoted the conversion of sugars to supply the necessary substrates for phenolic accumulation in fresh-cut melon.

Keywords: melon fruit; cutting; phenylpropanoid pathway; total phenolics; gene expression

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1. Introduction

Food is not only intended for consumption in our daily life but also to prevent diseases [1]. The high contents of nutrient substances in fruits and vegetables have been reported to guard against various diseases, such as cancer and cardiovascular diseases [2]. Increasing the contents of health-promoting substances in fruits and vegetables can increase their value and create more business opportunities. Thus, it is necessary to develop new technologies to enhance the health benefits of fresh products. In the past few years, the application of abiotic stresses in postharvest horticultural crops, such as ultraviolet light [1], wounding [3], and exogenous phytohormones [4], has been proposed as an effective and simple technology to induce biosynthesis of secondary metabolites beneficial to human health [5].

Cut fruit spoilage leads to important losses in minimally-processed fruits such as melon. Thus, understanding molecular mechanisms that trigger changes in cut fruits could open new possibilities for optimized processing and storage [6]. Melon (*Cucumis melo* L.) is a popular fruit containing bioactive substances important to human health, such as carotenoids, amino acids, vanillic acids, ascorbic acids, and trans-cinnamic acids [7,8]. It is cultivated and consumed worldwide because of its satisfying taste and health-promoting

effects [9]. Additionally, the requirement for fresh-cut melon fruit has increased recently on account of its convenience and freshness [10,11]. However, the rind, which is a natural barrier in melon fruit to maintain moisture and prevent microbial infection [12], is removed during fresh-cut processing. The peeling and high water content of melon accelerate the quality deterioration of fresh-cut melon, such as water-soaking and microbial growth [11,13]. Cutting of melon using unsharp tools could accelerate the translucency. In addition to cutting conditions, the quality and shelf life of fresh-cut melon are affected by variety, fruit maturity at harvest, and storage conditions [11,13,14].

Cut-wounding could be exploited as an effective and practical strategy to produce high content of bioactive compounds in postharvest fruits and vegetables [3,4,15], such as phenolic compounds, which can induce the production of secondary metabolites. Previous studies indicated that carrot [3], broccoli [16], and pitaya fruit [4] were used as model systems for exploring the phenylpropanoid metabolism affected by cut-wounding. Moreover, Contreras et al. [17] found that cut-wounding could effectively induce the biosynthesis of chlorogenic acid isomers in potato tubers. Phenolic compounds are excellent antioxidants, exhibiting anti-inflammatory and anti-cardiovascular disease effects [1]. Fruits and vegetables synthesize phenolic compounds through the phenylpropanoid pathway and primary metabolism pathways, including the shikimate pathway, Embden-Meyerhof-Parnas (EMP) pathway, and pentose phosphate pathway (PPP) [18,19]. Phenylalanine ammonia lyase (PAL), cinnamate-4-hydroxylase (C4H), and 4-coumarate-CoA ligase (4CL) are the critical enzymes involved in the biosynthesis of phenolic compounds. According to previous reports, these enzymes were activated by a series of biotic and abiotic stress-induced mechanisms [1,3,4]. Methyl jasmonate treatment in fresh-cut potato cubes could increase the activities and gene expressions of PAL, C4H, and 4CL, resulting in a higher content of flavonoids and phenolics [20]. In addition, Li et al. [4] found that cut-wounding enhanced the gene expressions of these three enzymes in pitaya fruit, accompanied by phenolic accumulation. Therefore, cutting of horticultural crops can trigger the mechanism of plant defense, which improves the contents of phenolic compounds, such as ferulic acid, caffeoylquinic acid, and their derivatives [3]. Surjadinata et al. [21] demonstrated that ethylene, jasmonic acid, and reactive oxygen species (ROS) participated in the wounding-induced phenolic accumulation, and ROS acted as the signal for ethylene synthesis, thus activating the biosynthesis of jasmonic acid and regulating phenolic metabolism. The water content of melon fruit is more than 90%; ultraviolet light could induce water ionization to produce ROS, leading to oxidative stress and further triggering phenylpropanoid metabolism [11,22].

In addition to the phenylpropanoid pathway, the EMP pathway and PPP utilize sugars to produce necessary intermediates and serve as substrates for the biosynthesis of phenolic compounds [19]. Moreover, the transformation of sugars through the EMP pathway can produce energy essential for physiological metabolism. Previous studies in potato [23] and apple [24] have proven that sucrose not only plays a role in regulating phenylpropanoid biosynthesis but also provides substrates for phenylpropanoid biosynthesis by producing hexose. Li et al. [25] also reported that methyl jasmonate, together with cut-wounding stress, synergistically induced the utilization and conversion of sugars to supply the necessary substrates and energy for the biosynthesis of phenolic compounds in pitaya fruit.

Nevertheless, most previous studies have focused on the accumulation of phenolic compounds induced by abiotic stress; little information is available regarding the relationship between wound-induced sugar utilization and phenolic accumulation in fresh-cut products [26]. In addition, the mechanism of phenolic accumulation via sugar metabolism is still unclear. Consequently, this study aimed to explore the molecular mechanism underlying sucrose metabolism and phenolic accumulation in fresh-cut melon fruit. Furthermore, the relation between phenolic accumulation and sucrose metabolism in melon fruit under cut-wounding stress was evaluated.

2. Materials and Methods

2.1. Fruit Materials and Treatments

The melon fruit 'Yugu' (*Cucumis melo* L. var. *cantalupensis* Nand.) was harvested at the commercially mature stage (35 days after flowering) and transported to the laboratory at Nanjing Agricultural University within 3 h from Xinghua, Jiangsu Province, China. The fruit was kept at 21 °C for 24 h. Fruits with uniform size and shape and without mechanical damage were selected for the study and divided into two groups (whole melon and fresh-cut samples). Fresh-cut samples were prepared and packaged into rigid plastic boxes as described previously [27] and stored at 15 °C. Fresh-cut samples (FC group) were sampled daily during storage for 4 days. Whole melon fruits (WF group) were stored at 15 °C and sampled on days 1, 2, 4, and 8. The storage temperature (15 °C) was applied in this study only to accelerate the response to wounding stress [28,29]. Each group contained three biological replicates, and each biological replicate contained ten random fruit samples. The sampled pulp was immediately frozen using liquid nitrogen and then stored at −80 °C for subsequent analyses.

2.2. Measurement of Soluble Sugars

Melon powder (2.0 g) from ten melon fruits was used for the extraction of soluble sugars according to our previous experimental method [27]. Sucrose, fructose, and glucose contents were determined according to our previous experimental method [27] using a high-performance liquid chromatography system with 10 µL of filtrate. The sugar contents were expressed as g kg^{-1} based on the fresh weight.

2.3. Determination of the Total Phenolic Content

Total phenolic content was assessed as described by Swain and Hillis [30] with slight modifications. Melon powder (3.0 g) from ten melon fruits was extracted with 25 mL of chilled methanol. The mixture was placed in a refrigerator at 4 °C for 12 h to extract phenolics fully. Next, the mixture was centrifuged at 12,000× *g* for 15 min at 4 °C. The reaction mixture containing 1.5 mL of deionized water, 1.0 mL of Folin-Ciocalteu reagent, 1 mL of 7.5% (*w*/*v*) Na_2CO_3, and 0.5 mL of supernatant was prepared to react for 2 h at 25 °C. The absorbance at 765 nm was measured using a UV-2802 spectrophotometer (Unico, Franksville, WI, USA). The total phenolic content was calculated with gallic acid as a standard and expressed as g kg^{-1} on a fresh weight basis.

2.4. Assessment of Enzyme Activities

The sucrose metabolism-related enzymes were extracted using melon powder (2.0 g) according to the method of Wu et al. [27] at 4 °C. The supernatant after dialysis was used as crude enzyme extracts for measuring sucrose phosphate synthase (SPS), sucrose synthase-synthesis (SS-s), sucrose synthase-cleavage (SS-c), neutral invertase (NI), and acid invertase (AI) according to our previously described methods [27]. One unit activity of SPS, SS-s, SS-c, NI, and AI was calculated as the amount of enzyme generating 1 µmol sucrose or glucose per hour, and the activity of the enzyme was expressed as U mg^{-1} on the protein content basis.

The activity of hexokinase (HXK) was assessed according to the method of Schaffer and Petreikov [31]. Melon powder (2.0 g) was ground with 4 mL of cold 50 mM HEPES-KOH buffer (pH 8.0, containing 2 mM EDTA, 5 mM $MgCl_2$, 0.1 mM leupeptin, 2.5 mM dithiothreitol, 2 mM benzamidine, 0.1% (*w*/*v*) BSA, 2% (*v*/*v*) glycerin, 1% (*v*/*v*) Triton X-100, and 4% (*w*/*v*) PVP). The extract mixture was centrifuged at 12,000× *g* at 4 °C for 10 min, and the supernatant was used for the activity measurement of HXK. The reaction mixture consisted of 0.1 mL enzyme extract and 0.9 mL of 50 mM HEPES-KOH (containing 10 mM glucose, 0.4 mM NADP, 1 U glucose-6-phosphate dehydrogenase, 2.5 mM ATP, and 4 mM $MgCl_2$). HXK activity was determined by the change in absorbance at 340 nm for 5 min. One unit activity of HXK was calculated as the amount of enzyme with a variation of 0.01 per min and expressed as U g^{-1} on the protein content basis.

PAL activity was assessed according to the method described by Ke and Saltveit [32]. Melon powder (2.0 g) was extracted using 5 mL of 50 mM borate buffer containing 2 mM of EDTA, 5 mM of β-mercaptoethanol, and 40 g L^{-1} of PVP (pH 8.8). The extract was placed in an ice bath for 10 min and then centrifuged at 12,000× *g* for 15 min at 4 °C. The reaction mixture consisting of 1.0 mL of enzyme supernatant, 2.8 mL of 50 mM borate buffer (pH 8.8), and 0.5 mL of 20 mM L-phenylalanine was incubated at 37 °C for 60 min, and then the reaction was terminated by adding 0.2 mL of 6 M HCl. One unit of PAL activity was calculated as the amount of enzyme with a variation of 0.01 per min at 290 nm and expressed as U g^{-1} based on the protein content.

C4H activity was assessed using the modified procedure of Lamb and Rubery [33]. Melon powder (2.0 g) was extracted using 5 mL of Tris-HCl buffer (50 mM, pH 8.9) containing 4 mM $MgCl_2$, 10 µM leupeptin, 5 mM ascorbic acid, 1 mM phenylmethylsulfonyl fluoride, 15 mM β-mercaptoethanol, 10% glycerol (*v*/*v*), and 0.15% PVP. The extract was placed in an ice bath for 10 min and then centrifuged at 12,000× *g* for 15 min at 4 °C. Next, the enzyme extract (0.4 mL) was incubated with 2.5 mL of 50 mM Tris-HCl buffer (pH 8.9, containing 2 mM NADP, 5 µM glucose 6-phosphate sodium, and 2 mM trans-cinnamic acid) at 25 °C for 30 min. The reaction was terminated by the addition of 0.2 mL of 6 M HCl. The absorbance was estimated at 340 nm before and after the incubation. One unit of C4H activity was defined as the amount of enzyme producing 1 µmol NADPH per min and expressed as U g^{-1} on the protein content basis.

4CL activity was assessed following the procedure reported by Knobloch and Hahlbrock [34] with slight modifications. Melon powder (2.0 g) was extracted using 5 mL of 50 mM Tris-HCl buffer (pH 8.0). The extract was placed in an ice bath for 10 min and then centrifuged at 12,000× *g* for 15 min at 4 °C. The reaction mixture consisting of 0.05 mL of 0.6 mM *p*-coumaric acid, 0.5 mL of 5 mM ATP, 2 mL of 5 mM $MgCl_2$, 0.05 mL of 0.4 mM coenzyme A, and 0.5 mL of the enzyme extract was incubated at 40 °C for 10 min. The absorbance was determined at 333 nm before and after the incubation. One unit of 4CL activity was calculated as the decrease in absorbance by 0.01 unit per min and expressed as U g^{-1} on the protein content basis.

2.5. Analysis of Expression of Key Genes Involved in Sucrose Metabolism and the Phenylpropanoid Pathway

The genes involved in sugar metabolism and the phenylpropanoid pathway were identified from the CuGenDB (http://cucurbitgenomics.org/) (accessed on 2 May 2021) and were analyzed through the transcriptome. The total RNA and first-strand cDNA were obtained according to our previous experimental method [27]. The gene-specific primers (Table S1) were designed using Primer 6.0 software (PREMIER Biosoft International, San Francisco, CA, USA); the specificity of primers was examined by gel-electrophoresis and melting curves. β-actin was used as the internal control gene. The real-time quantitative reverse transcription PCR (qRT-PCR) procedure and data analysis were performed following our previous experimental method [27].

2.6. Statistical Analysis

Data were expressed as the mean ± SE (standard error) of three replicates. The data from fresh-cut and whole melon samples were compared via one-way analysis of variance (ANOVA) and Student's *t*-test using SPSS 19.0 (SPSS Inc., Chicago, IL, USA), wherein $p < 0.05$ was considered statistically significant.

3. Results

3.1. Changes in Soluble Sugars and Total Phenolic Content

The changes in soluble sugar content (sucrose, fructose, and glucose) are shown in Figure 1. The sucrose content of WF group showed an initial increasing and then decreasing trend and reached the maximum value on the second day of storage. However, the sucrose content in FC group decreased with the storage period and showed a noteworthy lower

level in comparison with that of WF group (Figure 1A, $p < 0.01$). The fructose and glucose contents in WF group decreased gradually during the storage period, while those of FC group increased initially, followed by a noteworthy decrease after a longer storage time. Moreover, FC group maintained higher levels of glucose and fructose than WF group only during the initial two days of storage (Figure 1B,C, $p < 0.05$). The total phenolic content of WF group changed slightly during storage, while that of FC group suddenly increased after cutting and maintained at a significantly higher level at the late storage stage in comparison with WF group (Figure 1D, $p < 0.05$). It could be speculated that cutting accelerated the sucrose degradation and led to the increase in hexoses at the early stage of storage, accompanied by the accumulation of phenolics.

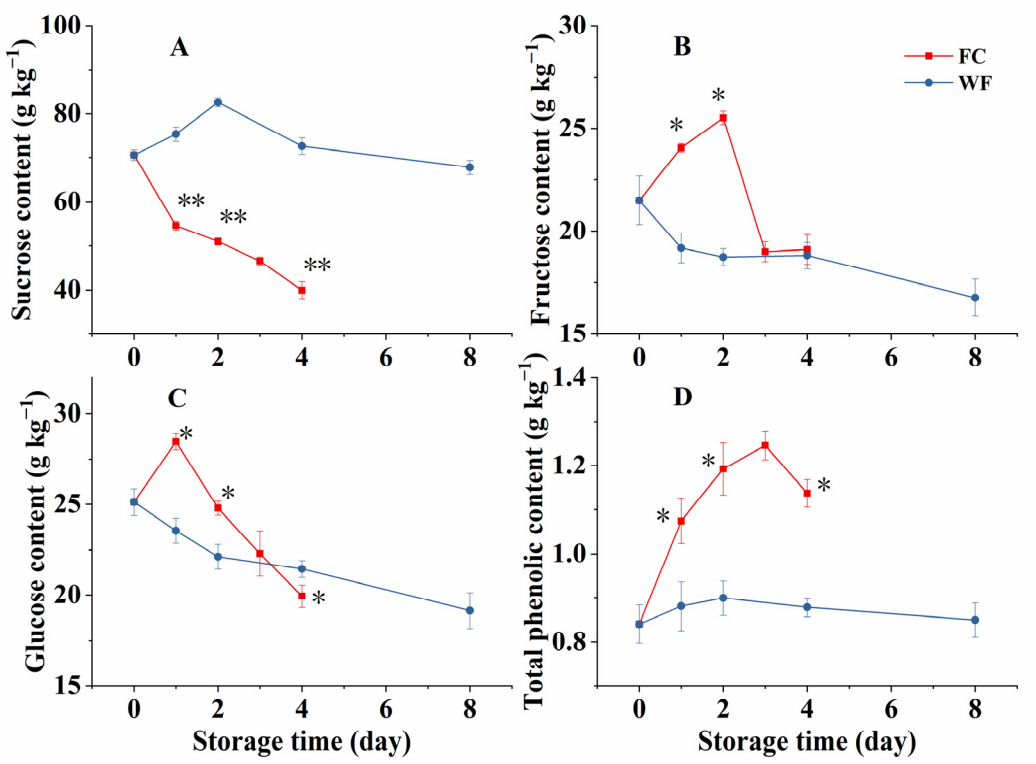

Figure 1. Effect of cutting on the contents of sucrose (**A**), fructose (**B**), glucose (**C**) and total phenolic (**D**) in melon fruit during storage (15 °C). FC and WF respectively represent fresh-cut and whole melon fruit. The values are expressed as means ± SE of three replicates. * and ** indicate statistically significant differences ($p < 0.05$ and $p < 0.01$ respectively) according to Student's *t*-test at each sampling point.

3.2. Activities of Key Enzymes Involved in Sucrose Metabolism

As shown in Figure 2A, SPS activity in the two groups decreased during storage. However, it decreased rapidly and displayed a remarkably lower level in FC group than in WF group during storage ($p < 0.05$). Similar to SPS, SS-s activity showed a downward trend during storage. The SS-s activity of FC group was lower than that of WF group on the second and fourth days of storage (Figure 2B, $p < 0.05$). Contrary to SS-s and SPS activities, the activities of SS-c, AI, NI, and HXK enhanced in FC group and maintained higher levels in comparison with WF group throughout the entire storage period (Figure 2C–F, $p < 0.05$).

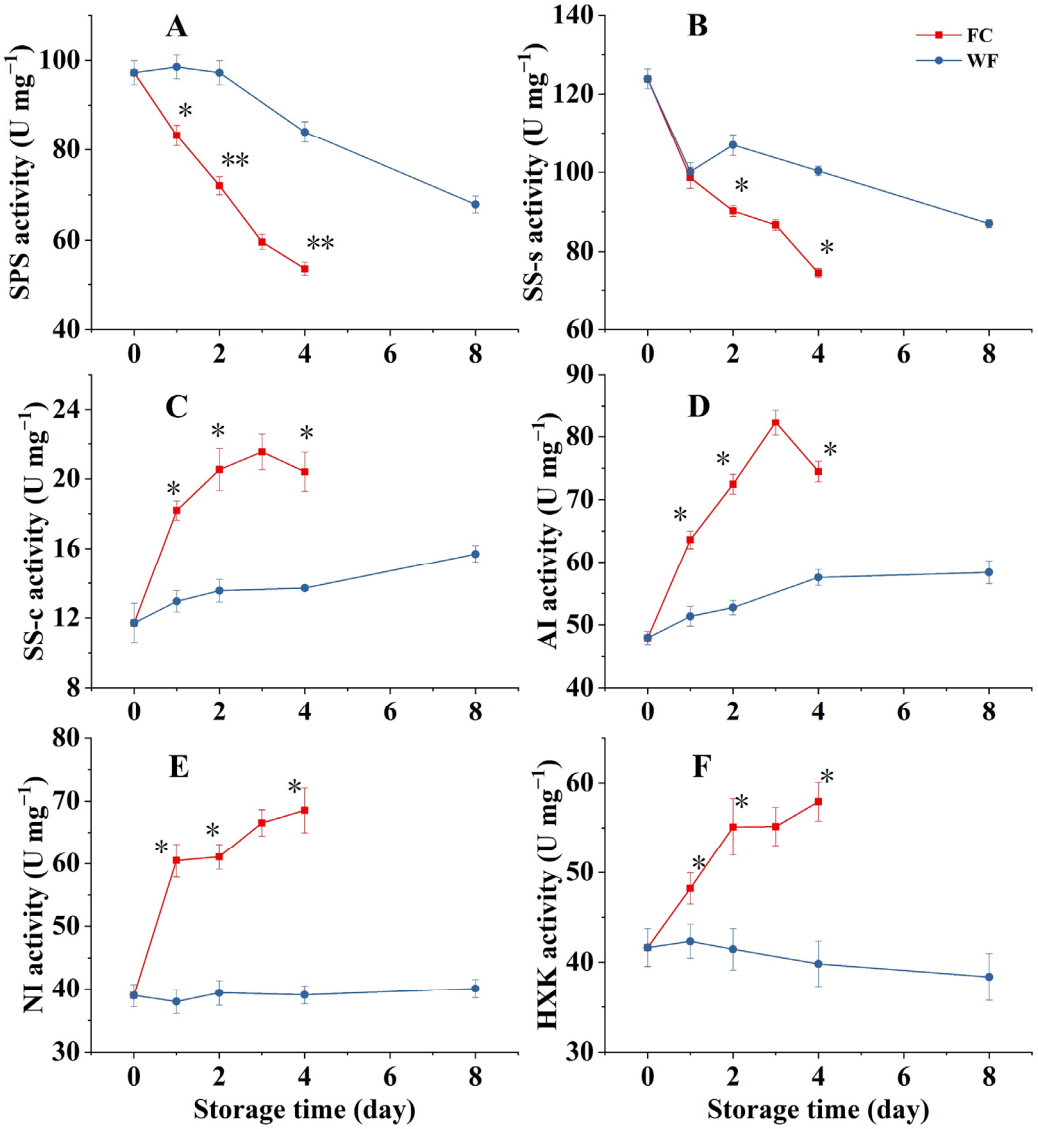

Figure 2. Effect of cutting on the activities of (**A**) sucrose phosphate synthase (SPS), (**B**) sucrose synthase-synthesis (SS-s), (**C**) sucrose synthase-cleavage (SS-c), (**D**) acid invertase (AI), (**E**) neutral invertase (NI) and (**F**) hexokinase (HXK) in melon fruit during storage (15 °C). FC and WF respectively represent fresh-cut and whole melon fruit. The values are expressed as means ± SE of three replicates. * and ** indicate statistically significant differences ($p < 0.05$ and $p < 0.01$ respectively) according to Student's *t*-test at each sampling point.

3.3. Activities of Key Enzymes Involved in the Phenylpropanoid Pathway

The PAL activity of WF group remained stable during storage, except for a transient decrease at day 2. However, the PAL activity of FC group increased with storage time and was noteworthy higher than that of WF group until the end of storage (Figure 3A, $p < 0.05$). The C4H activity of WF group increased after two days of storage and then changed slightly at the late stage of storage. Similar to PAL, the C4H of FC group increased significantly during storage and was higher than that of WF group (Figure 3B, $p < 0.05$). The 4CL activity of WF group showed a gradual decrease during storage. However, it increased sharply from day 0 to day 4 and then remained stable in FC group, which was consistently higher compared with that of WF group (Figure 3C, $p < 0.05$).

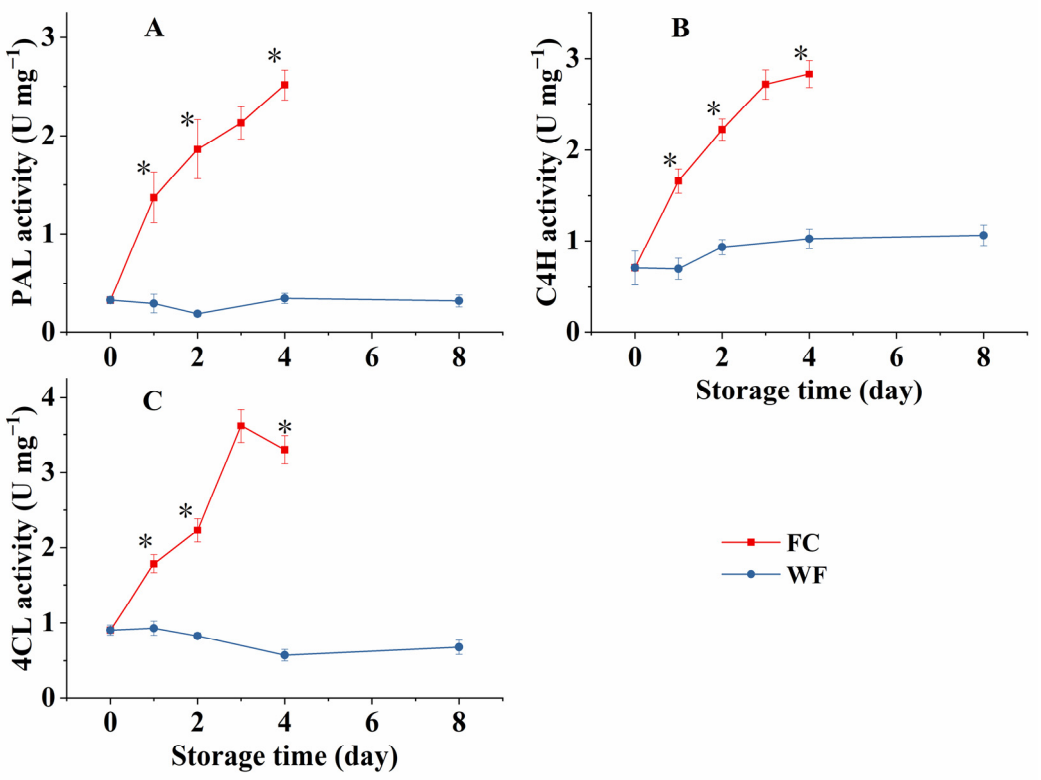

Figure 3. Effect of cutting on the activities of (**A**) phenylalanine ammonia-lyase (PAL), (**B**) cinnamate 4-hydroxylase (C4H), and (**C**) 4-coumarate: CoA ligase (4CL) in melon fruit during storage (15 °C). FC and WF respectively represent fresh-cut and whole melon fruit. The values are expressed as means ± SE of three replicates. * indicate statistically significant differences ($p < 0.05$) according to Student's *t*-test at each sampling point.

3.4. Expressions of Genes Involved in Sucrose Metabolism

As shown in Figure 4, the expression of *CmSS1* in WF group increased with storage time. However, the *CmSS1* expression in FC group was consistently higher than that in WF group during storage ($p < 0.01$). Contrary to *CmSS1*, the expressions of *CmSS2/3* decreased in the FC group during storage compared with WF group ($p < 0.05$). The expression patterns of SPS genes (*CmSPS1/2/4*) in the WF group were different during storage (Figure 4). The *CmSPS1* expression changed slightly in WF group, except for its up-regulation on day 4, while its expression decreased in FC group during storage and exhibited notably lower levels compared with WF group ($p < 0.01$). Moreover, the expressions of *CmSPS2/4* in WF group exhibited a decreasing trend during storage, while their decrease in FC group was accelerated; FC group displayed lower levels of their expressions compared with WF group throughout the entire storage period ($p < 0.05$).

The expressions of AI genes (*CmAI1/2*) increased during melon storage and were consistently higher in FC group (Figure 4, $p < 0.01$). The expression of *CmNI1* increased in the FC and WF groups during the early stage of storage, followed by a decrease. However, the expression of *CmNI1* was higher in FC group than in WF group just during the initial two days of storage (Figure 4, $p < 0.05$). Cutting stimulated *CmNI2* expression, and it was higher in FC group than in WF group until the end of storage (Figure 4, $p < 0.01$). The expression of *CmHXK1* in WF group decreased from day 0 to day 1 and remained stable until day 6, followed by a decrease on day 8. Its expression in FC group increased during the first two days of storage and then decreased. However, fresh-cut melon maintained a higher level of *CmHXK1* expression in comparison with WF group (Figure 4, $p < 0.01$).

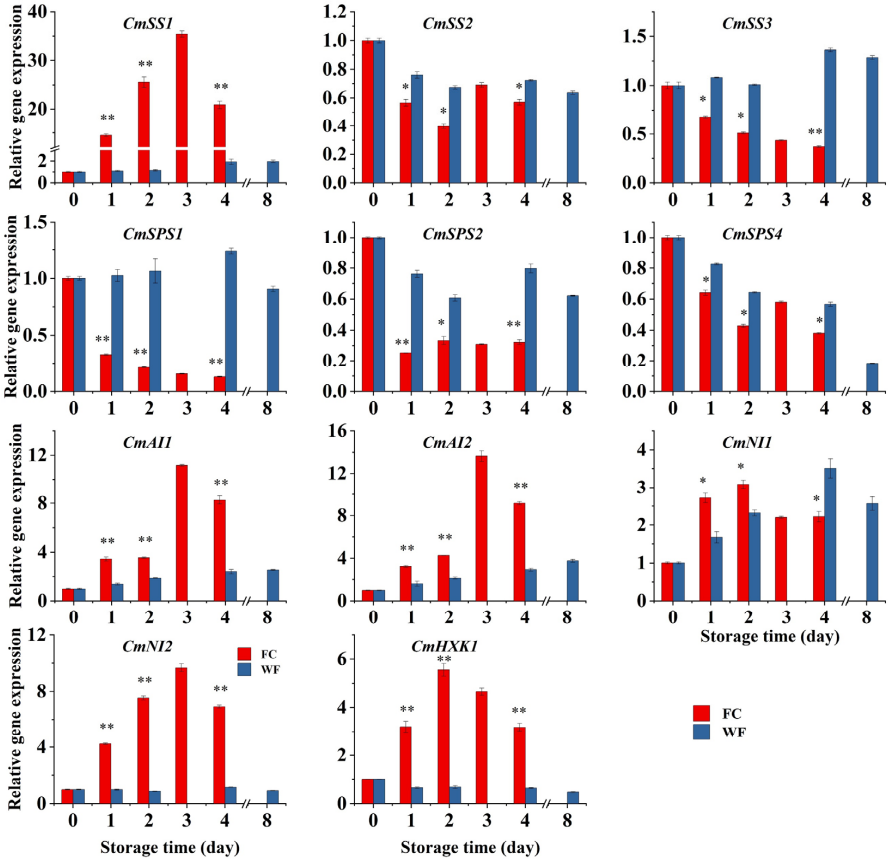

Figure 4. Effect of cutting on the relative gene expressions of sucrose synthase (*CmSS1/2/3*), sucrose phosphate synthase (*CmSPS1/2/4*), acid invertase (*CmAI1/2*), neutral invertase (*CmNI1/2*), and hexokinase (*CmHXK1*) in melon fruit during storage (15 °C). FC and WF respectively represent fresh-cut and whole melon fruit. The values are expressed as means ± SE of three replicates. * and ** indicate statistically significant differences ($p < 0.05$ and $p < 0.01$ respectively) according to Student's *t*-test at each sampling point.

3.5. Expressions of Genes Involved in the Phenylpropanoid Pathway

The transcript levels of PAL genes (*CmPALs*) of WF group showed different expression patterns during storage. The expressions of *CmPAL1/2*, *CmPAL4*, and *CmPAL6/7/8/9* decreased gradually, while those of *CmPAL3/5* changed slightly in WF group during storage (Figure 5). Moreover, cutting melon fruit increased the expressions of *CmPALs* to varying degrees during storage ($p < 0.01$). The expressions of *CmPAL1/2/4/5* in FC group increased during the first two days and then decreased at the late stage of storage, while the *CmPAL6* expression increased with the storage period. The expressions of *CmPAL3/7/8/9* in FC group increased until day 3 and decreased afterward. In short, the expressions of *CmPALs* were higher in FC group than in WF group throughout the entire storage period (Figure 5, $p < 0.01$).

As shown in Figure 6, the expression of *CmC4H1/4* in WF group increased in the initial 4 days and decreased thereafter, while that of *CmC4H2* decreased with the storage time and *CmC4H3* changed slightly, except for an increase on day 4. Similar to *CmPALs*, the expressions of *CmC4Hs* in FC group were also stimulated and exhibited higher levels compared with WF group ($p < 0.01$). The expressions of *Cm4CL1/2* in WF group decreased gradually during storage, while those in FC group were enhanced and maintained at higher levels in comparison with WF group (Figure 6, $p < 0.01$). Although *Cm4CL3* expression of WF group remained stable during storage, its expression was stimulated and enhanced by cutting. Moreover, *Cm4CL3* expression was higher in FC group than in WF group throughout the entire storage period (Figure 6, $p < 0.05$).

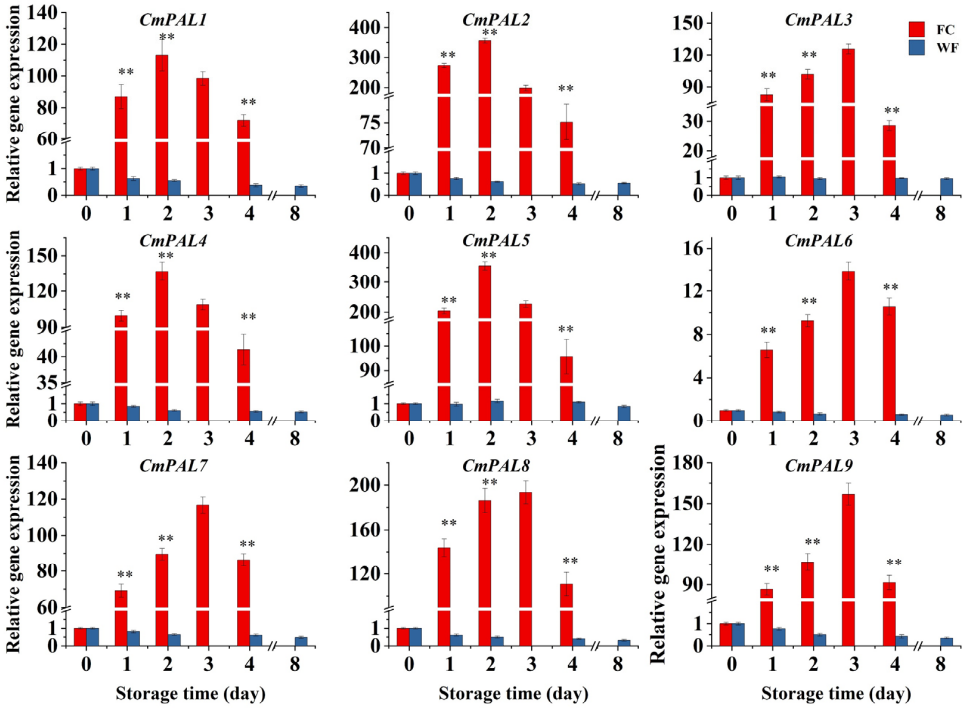

Figure 5. Effect of cutting on the relative gene expressions of phenylalanine ammonia lyase (*CmPALs*) in melon fruit during storage (15 °C). FC and WF respectively represent fresh-cut and whole melon fruit. The values are expressed as means ± SE of three replicates. ** indicate statistically significant differences ($p < 0.01$) according to Student's *t*-test at each sampling point.

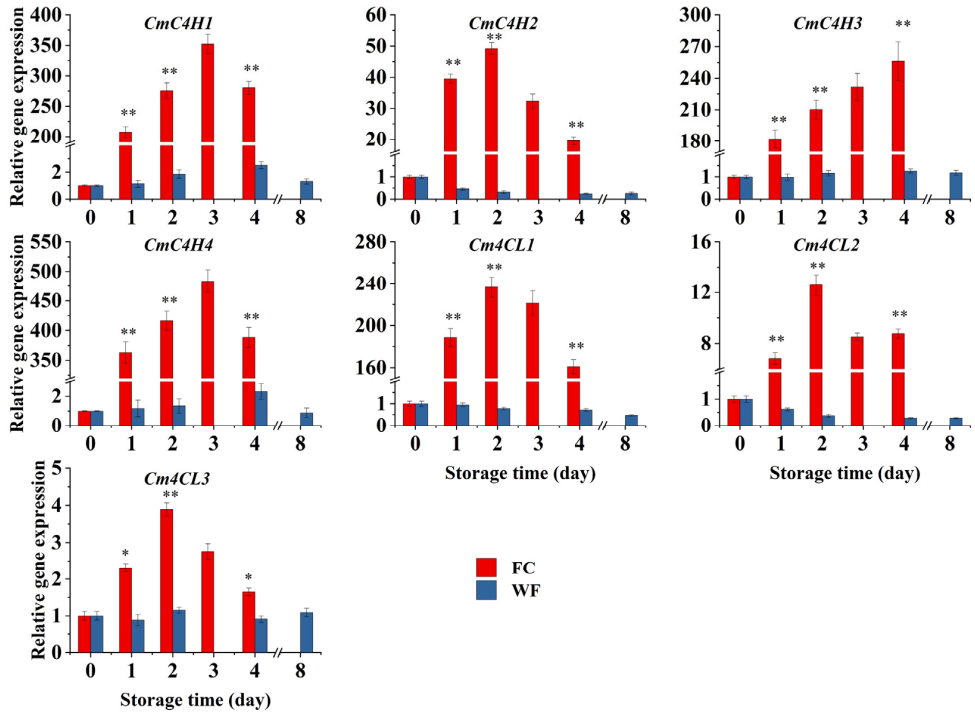

Figure 6. Effect of cutting on the relative gene expressions of cinnamate-4-hydroxylase (*CmC4H1/2/3/4*) and 4-coumarate-CoA ligase (*Cm4CL1/2/3*) in melon fruit during storage (15 °C). FC and WF respectively represent fresh-cut and whole melon fruit. The values are expressed as means ± SE of three replicates. * and ** indicate statistically significant differences ($p < 0.05$ and $p < 0.01$ respectively) according to Student's *t*-test at each sampling point.

4. Discussion

Numerous previous studies have proven that cut-wounding can induce phenolic accumulation and improve the nutrient content and antioxidant capacity in postharvest fruits and vegetables, such as potato [17], carrot [3], pitaya fruit [25], red prickly pears [35], and broccoli [16]. There is a lack of studies on species from the Cucurbitaceae family regarding cut-wounding induced phenolic accumulation. Although cutting of melon accelerated the browning and decreased the firmness (data not shown), which led to the lower commercial value of fresh-cut melon at the end of storage [27,36]. Interestingly, cutting induced the accumulation of phenolics in fresh-cut melon (Figure 1). Primary metabolism is vital in regulating the biosynthesis of secondary metabolites. However, the mechanism of the effect of cut-wounding on the substrate level in primary metabolism is often ignored [10,21,26]. Our results indicated that the cutting of melon accelerated sucrose decomposition and then provided more hexoses (fructose and glucose) for fresh-cut melon during the early stage of storage, which was accompanied by the enhancement of the phenylpropanoid pathway and increased phenolic accumulation (Figures 1–3).

Sugar, the important quality index of horticultural commodities, acts as a crucial substrate in the primary metabolism of plants. The consumption and transformation of sugars (e.g., sucrose, fructose, and glucose) produce many necessary precursors used as substrates for phenolic biosynthesis in the shikimate pathway [18,25]. In this study, cutting melon fruit accelerated sucrose decomposition, which generated higher contents of fructose and glucose in fresh-cut melon during the initial two days of storage (Figure 1); this result is similar to the findings of previous works on fresh-cut apple [37] and fresh-cut melon [27]. Sugars are crucial chemical compounds in horticultural crops as they help provide nutrition, release energy, and form the flavor of fruit [38]. The production of anthocyanin is accompanied by sugar accumulation during fruit growth. Exogenous sucrose treatment increased the anthocyanin biosynthesis in postharvest strawberry fruit by activating PPP and phenylpropanoid pathway [39]. The entry of carbon from sucrose into cellular metabolism in horticultural crops is catalyzed by AI, NI, or SS-c [40]. In addition, some abiotic stresses, including cut-wounding, ultraviolet light, storage temperature and hot air treatment, may change sucrose metabolism by affecting NI, AI, and SS-c [27,38,41,42]; this can affect the secondary metabolism of plants and improve their resistance. In this study, the activities of SS-c, AI, and NI in fresh-cut melon enhanced, and those of SS-s and SPS decreased, accompanied by the high expressions of key genes involved in sucrose degradation and lower expression of genes in sucrose synthesis (Figures 2 and 4). This was consistent with the result of exogenous sucrose treatment enhancing the transcription levels of invertase for mediating flavonoid biosynthesis in plants [23,43]. Thus, these results suggested that cut-wounding expedited sucrose decomposition via increasing AI, NI, and SS-c activities and their transcriptional profiles, leading to increased glucose and fructose levels. A similar result was also reported in postharvest peaches infected by *Monilinia fructicola* [44].

Moreover, the gene expression and activity of HXK were enhanced in fresh-cut melon. HXK is the key enzyme of the EMP pathway in plants and plays an important role in sensing sugar signals and participating in response to abiotic stress [45,46]. It phosphorylates hexose to decompose glucose and fructose. The glucose 6-phosphate generates phosphoenolpyruvate (PEP) via the EMP pathway and then to erythrose-4-phosphate (E4P) in the PPP. PEP and E4P are key substrates for the shikimate pathway, and the products are ulteriorly transformed into phenolic compounds through the phenylpropanoid pathway [19,47]. In addition, the EMP pathway is important for acquiring energy in plants; the higher gene expression and activity of HXK indicate that cut-wounding can enhance the utilization and conversion of sugars, providing necessary substrates and energy for downstream metabolic pathways [19,25,44].

Phenolics are mainly produced by the phenylpropanoid pathway in plant tissues after mechanical injury, and this pathway also plays a crucial role in plant resistance to external stresses [4,48]. In the phenylpropanoid pathway, three enzymatic conversions of PAL,

C4H, and 4CL could redistribute the carbon flow from primary metabolism, converting phenylalanine into the hydroxycinnamoyl-CoA thioester capable of entering downstream pathways [49]. PAL, C4H, and 4CL are activated when plants resist biotic and abiotic stresses [4,48]. Liu et al. reported [50] that acibenzolar-S-methyl treatment enhanced the activities of PAL, C4H, and 4CL for activating the phenylpropanoid pathway in melon fruit, which enhanced the strength of cell wall and prevented microbial invasion. In our study, cutting of melon increased the activities of PAL, C4H, and 4CL (Figure 3). The results were consistent with those obtained in the studies on fresh-cut pitaya fruit [4], fresh-cut potato cubes [20], and fresh-cut strawberries [51], wherein the activities of all three enzymes were enhanced by cut-wounding. Together with the data of this work, it indicated that cutting of melon could regulate the phenylpropanoid pathway, leading to phenolic accumulation, as shown by the increase in total phenolic content in the fresh-cut melon (Figure 1).

The increased activity of a plant enzyme is often accompanied by increased expression of its related gene. The expressions of *HuPAL*, *HuC4H*, and *Hu4CL* in pitaya fruit were enhanced by cut-wounding stress, accompanied by increased activities of related enzymes [4]. To further investigate how cut-wounding could accurately regulate phenylpropanoid metabolism and induce the accumulation of phenolics in melon fruit, the changes in gene expression of these three enzymes in the phenylpropanoid pathway were analyzed. It was found that cutting melon up-regulated the expressions of *CmPAL1-9*, *CmC4H1-4*, and *Cm4CL1/2/3* (Figures 4 and 5), which was in accordance with the corresponding enzyme activity. These results were in agreement with a previous study on methyl jasmonate treatment increasing the gene expression levels of PAL, 4CL, and C4H to enhance the resistance of fresh-cut potato cubes [20]. In short, cutting melon induced phenolic biosynthesis by enhanced phenylpropanoid metabolism, indicated by increased activities and gene expressions of related enzymes. The expressions of PAL, 4CL, and C4H genes in plants have obvious tissue specificity, which generally consists of small multigene families. The PAL of *Arabidopsis* is encoded by *AtPAL1-4* [52]. The 4CL homologs in plants have different degrees of binding to hydroxycinnamic acid derivatives, and the related gene expression patterns are also significantly different. The *At4CL1/2* participated in lignin synthesis in *Arabidopsis*, as revealed by gene co-expression analysis, while *At4CL3* was associated with flavonoid synthesis [53]. Furthermore, the increased gene expressions in our experiments indicated that lignin and other secondary metabolites might be enriched in fresh-cut melon, which was also found in potato tubers [54] and injured tomato fruit [55]. Li et al. [56] reported that hot air pretreatment in pitaya fruit could affect the phenylpropanoid metabolism to alleviate the browning caused by cut-wounding, which was due to the enhanced gene expressions and activities of PAL, 4CL, and C4H. The expressions of genes in the phenylpropanoid pathway were affected by ultraviolet irradiation, which has been revealed in injured carrots using transcriptomic analysis [57]. However, it is necessary to further explore how these genes accurately regulate the biosynthesis of phenolics and the defense response in fruits and vegetables. This study offers new insight into the molecular mechanism of sucrose metabolism and phenylpropanoid pathway in injured melon fruit and provides a molecular basis for further exploring the information of phenolic metabolism induced by cut-wounding.

5. Conclusions

This work explored the molecular changes underlying the sucrose and phenylpropanoid metabolism during the storage of fresh-cut melon. The cutting of melon accelerated sucrose decomposition, which generated higher contents of fructose and glucose in fresh-cut melon at the early stage of storage. This was confirmed by the higher activities of AI, NI, and SS-c and the up-regulated expressions of *CmAI1/2*, *CmNI1/2*, and *CmSS1* in fresh-cut melon. Simultaneously, the activities of SS-s and SPS and the expressions of *CmSS2/3* and *CmSPS1/2/4* were inhibited in fresh-cut melon, resulting in a higher hexose content. However, cutting melon also accelerated the transformation of hexose due to the higher HXK activity and *CmHXK1* expression level. Moreover, the phenylpropanoid metabolism in melon was enhanced by

cutting as indicated by the higher activities of PAL, C4H, and 4CL and the up-regulated expressions of *CmPAL1-9*, *CmC4H1-4*, and *Cm4CL1/2/3*, leading to the higher content of total phenolics. In brief, cutting melon fruit can promote the utilization and conversion of sugars to supply the necessary substrates for wound-induced phenolic accumulation in fresh-cut melon. To explain how cut-wounding promoted the conversion of sugars to supply necessary substrates for phenolic accumulation in melon fruit, a hypothetical model was developed, as shown in Figure 7. This useful information will be a benefit for enhancing the phenolic content during the processing and storage of fresh-cut melon.

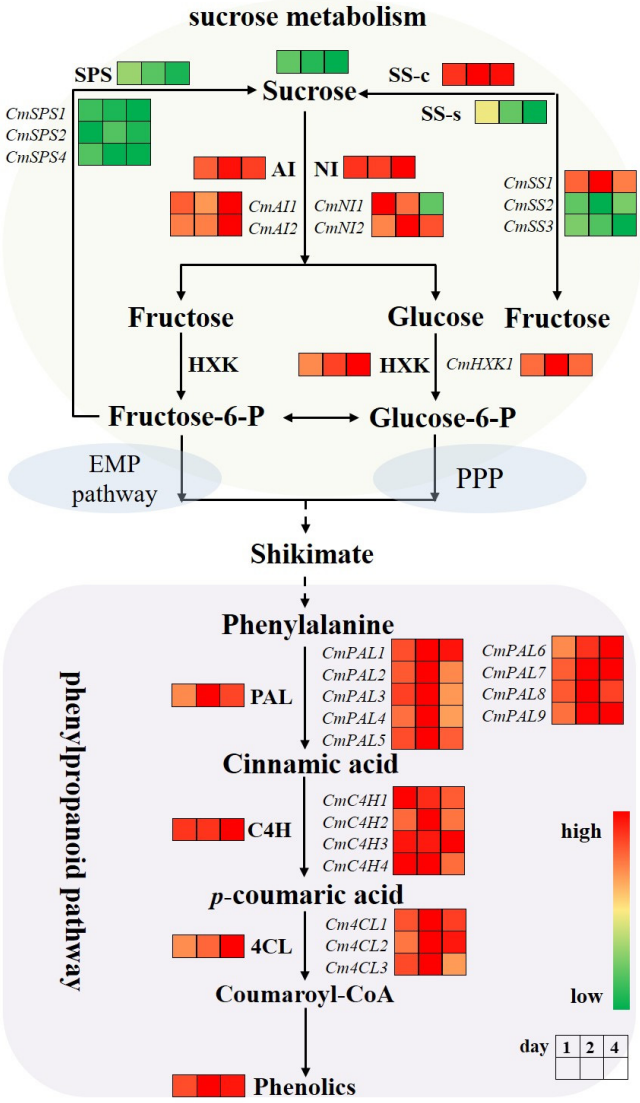

Figure 7. A hypothetical model to explain how cut-wounding promoted the conversion of sugars to supply necessary substrates for phenolic accumulation in melon fruit during storage at 15 °C. Red and green respectively represent the significant increase and decrease in metabolite content, enzyme activity and gene expression, while yellow means no significant difference ($p < 0.05$). All the significant differences are compared with whole melon fruit.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/horticulturae9020258/s1, Table S1. Primers used for quantification of mRNA levels by qRT-PCR.

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