Effects of Ultraviolet-C Pretreatment on Sugar Metabolism in Yellow Peaches during Shelf Life

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Abstract. To investigate the influence of ultraviolet-C (UVC) radiation pretreatment on the sugar metabolism of yellow peaches (cv. Beionong2 × 60–24–7) during storage, the concentrations of soluble sugar (sucrose, fructose, glucose, and sorbitol), and related gene expression were determined. During UVC pretreatment, peaches were subjected to a dose of 4 kJ·m⁻² when they were placed at 15 cm under a UVC lamp tube for 10 minutes at 25 °C. Then, they remained at 15 ± 2 °C for 10 days. Peaches stored at 15 ± 2 °C immediately after picking were used as the control group (CG). UVC pretreatment reduced the ethylene production rate and resulted in a significant increase in the accumulation of sucrose during days 2 to 8 of the storage period, followed by a lower concentration of fructose and glucose and the upregulation of PpaSS1. The expression levels of PpaSPS2, PpaSS1, and PpaST3 were significantly correlated with fructose concentration, and those of PpaSPS2 and PpaST2 were significantly correlated with glucose concentration. The enzyme activity of sucrose phosphate synthase (SPS) was positively correlated with PpaSPS2, PpaSS2, and PpaST2. The enzyme activities of sucrose synthase (SS), acid invertase (AI), and neutral invertase (NI) were positively correlated with PpaSS1, PpaST1, and Ppani, respectively. Expressions of PpSPS1 and PpSPS2 in UVC-pretreated peaches were upregulated on storage days 8 and 2, and there was a UVC-induced peak in SPS activity on storage days 4 and 8, which resulted in the rapid accumulation of sucrose. UVC pretreatment could upregulate the gene expression of PpaSS1 on day 2, which could improve and maintain the quality of peaches for consumption.

Jinxiang yellow peach (*Prunus persica* L. Beionong2 × 60–24–7) is a yellow flesh peach cultivar; because of its excellent sensory properties, such as golden flesh color, sweet and attractive fragrance, and high economic value, it has become an important cultivar in the Yangtze River Delta (Zhou et al., 2016). However, consumers are bothered by lower quality and storage disorders during postharvest handling and ripening in the market (Byrne, 2005). The fruit flavor is one of the most vital traits of fruit quality and is primarily dictated by the concentration of sugars (Kader, 2008; Zhou et al., 2018). Regulating

fruit sugar metabolism has become an important method of maintaining the quality of postharvest peach fruit (Zhu et al., 2010). The main soluble sugars in peaches are sucrose, fructose, glucose, and sorbitol, which are regulated by vacuolar acid invertase (AI), neutral invertase (NI), sucrose phosphate synthase (SPS), and sucrose synthase (SS) (Bianco and Rieger, 2002; Han et al., 2018). As a pivotal enzyme in sucrose biosynthesis, the enhancement of SPS activity is often associated with sucrose accumulation (Ni et al., 2011). SS acts principally on cleavage, although it has a dual role (Fallahi et al., 2008), and sucrose can be catalyzed by AI/NI or SS to generate fructose, glucose, or UDP-glucose (UDP-Glc) (Duque et al., 1999).

Targeted breeding toward tastier peach cultivars and selection for those that develop flavor early, even before the onset of ripening and softening, could potentially improve peach consumption as well as some postharvest technology (Han et al., 2018). Changes in sunlight composition can induce phytochrome (PHY) and cryptochrome (CRY)-mediated plant responses and improve fruit quality (Minas et al., 2018). Ultraviolet-C hormesis consists of the use of low doses of shortwave ultraviolet radiation with the objective of promoting desirable responses in living organisms

(Stevens et al., 2005), which could reduce the use of chemicals to achieve the same response (Issa-Zacharia et al., 2010). The use of UVC has been investigated for its role in reducing damage caused by the fungus *Botrytis cinerea* in bell peppers (Mercier et al., 2001), reducing CI and decay in peppers (Vicente et al., 2005), reducing lesion development on mushroom surfaces (Guan et al., 2012), delaying tomato ripening (Barka, 2001), and improving fruit quality (Artès et al., 2009; Charles, 2008; Shama and Alderson, 2005). Gonzalez-Aguila et al. (2004) reported that concentrations of putrescine, spermine, and spermidine in peaches were higher with improved quality after treatment with UVC for 3 to 5 min. Scattino et al. (2014) showed that ultraviolet-B (UVB) radiation could influence the concentration of several polyphenols in peaches through the molecular regulation of their biosynthetic genes. In a previous study, untreated pears were found to be superior in flavor and sweeter than ultraviolet-treated pears (Syamaladevi et al., 2014). This is in contrast to results reported by Manzocco et al. (2011), who found a higher flavor score for UVC-treated cut melons than for control cut melons. Santin et al. (2018) demonstrated that UVB reduced concentrations of carotenoids and most lipids and increased some biosynthetic intermediates and degradation products, some of which are known for their positive effects on human health.

Most studies showed that UVC treatment could improve the quality of fruit and is a good technological application; however, these studies were all limited to the physiological/biochemistry level, more sophisticated methods of flavor analysis, and more recent studies of the relationship between preharvest factors and fruit quality. Few systematic studies of the effect of UVC pretreatment on sugar metabolism at substrate, enzyme, and regulation levels, together with associated gene expression levels, are available for peaches and their shelf life. In this study, the concentrations of soluble sugars and related gene expressions in peaches pretreated with UVC were determined to elucidate how UVC affects expression levels of genes associated with sugar metabolism during shelf life. The findings are expected to improve or maintain the shelf-life quality of peaches by using UVC pretreatment to increase peach fruit consumption.

Materials and Methods

Plant materials. Jinxiang yellow peaches (*Prunus persica* L. Beionong2 × 60–24–7) were picked from an orchard located in the Fengxian District of Shanghai, China (lat. 30.92°N, long. 121.47°E). The tree age was 9 years, and fruit was carried out at the crown circumference height of 12 trees for ≈1 to 2 m randomly, which were bagged with yellow bags. Peaches were picked on 20 June 2017, when they were at a commercially mature stage (maturity stage of seven or eight). Uniform peaches with no obvious defects or

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mechanical wounds were randomly divided into three groups, with each containing 100 peaches. There were three replicates of each group, for a total of 300 peaches tested per group. The peaches were transported to the experimental laboratory at the Shanghai Academy of Agricultural Sciences within 30 min of picking.

Experimental design. In the control group (CG), peaches were stored at an ambient temperature ($15 \pm 2^\circ\text{C}$) and 75% to 80% relative humidity for 10 d. Peaches in the UVC treatment group were subjected to a hormetic UVC dose at $4 \text{ kJ}\cdot\text{M}^{-2}$ when they were placed 15 cm under a UVC lamp tube for 10 min at 25°C . After treatment with UVC, peaches were stored under the same conditions as the control peaches ($15 \pm 2^\circ\text{C}$ and 75% to 80% relative humidity) for 10 d. Storage for the experimental design was a simulation of the shelf and the transportation environment in China. Samples of 20 peaches were randomly collected from each replicate every 2 d. Liquid nitrogen was used to immediately freeze peach mesocarps from each group; then, the frozen flesh was stored at -80°C for a subsequent analysis of physiological and biochemical indexes and gene expression.

Measurements. The ethylene production rate was measured following the method described by Khan (2008) at 15°C , with slight modifications. Three replicates of five peaches each were enclosed in 10-L glass jars capped with rubber stoppers for 1 h at each sampling time. Headspace gas (1 mL) was removed from the jars using a syringe and was injected in the inlet of a gas chromatograph (Agilent GC7890A; Agilent Technologies, Santa Clara, CA) fitted with a flame ionization detector (FID). The results were expressed as $\text{nL}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$.

Respiration intensity. Respiration intensity was measured based on the amount of released CO_2 and determined using an IR CO_2 gas analyzer (GXH-3010E; Nuojin Instruments Inc., Changzhou, China) as described by Huan et al. (2016). Three replicates of three fruits each were used to determine the respiration rate. The results were expressed as $\text{mg}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$.

Sugar content. After grinding each sample in liquid nitrogen, a 0.5-g sample was placed into a centrifuge tube and 5 mL of extract was prepared by adding anhydrous ethanol and 0.4% metaphosphoric acid at 80:20 v/v. Samples were soaked for 24 h and then centrifuged for 10 min at $10,000 g_n$. One gram of liquid supernatant was concentrated and re-dissolved in 0.5 mL ultrapure water to determine sucrose, fructose, glucose, and sorbitol concentrations (mg/g) using an Agilent 1100 high-pressure liquid chromatography (HPLC) system (Agilent Technologies). To quantify the sugar concentration, a CARBOSep CHO-620 capillary column ($10 \mu\text{m} \times 6 \text{ mm} \times 250 \text{ mm}$) (Transgenomic, Inc., New Haven, CT) and a differential refraction detector were used. The column temperature was 80°C , and $15 \mu\text{L}$ of sample was injected. The mobile phase was ultrapure water.

Analysis of enzyme activity. Frozen peach flesh (1.5 g) was ground in a chilled mortar with 5 mL of 100 mM Tris-HCl buffer ($\text{pH} = 7.0$) containing 5 mM MgCl_2 , 2 mM EDTA, 2% ethanediol, 0.2% bovine serum albumin, 2% PVP, and 5 mM DTT. Tissue mixtures were centrifuged at $10,000 g_n$ for 30 min. The supernatant was used to determine activities of AI, NI, SS, and SPS.

The reaction system of AI was composed of 80 mM sodium phosphate ($\text{pH} = 4.7$), 50 mM sucrose, and crude enzyme. After incubating at 30°C for 30 min, the reaction was ended by boiling for 3 min. Subsequently, 1 mL of 3, 5-dinitrosalicylic acid (DNS) was added to the reaction system, and the mixture was boiled for an additional 5 min to determine the concentration of glucose generated by this reaction using an ultraviolet spectrophotometer at 540 nm. Control reactions contained the boiled extract. The assay of NI activity was similar to that of AI activity, except the reactions were conducted at $\text{pH} 7.0$. Enzyme activity was expressed as $\text{ng}\cdot\text{min}^{-1}\cdot\text{g}^{-1}$ fresh weight (FW).

The reaction mixture of SPS consisted of 100 mM Tris-HCl buffer ($\text{pH} 7.0$), 10 mM fructose-6-phosphate, 2 mM EDTA, 5 mM magnesium acetate, 5 mM DTT, 10 mM UDP-Glc, and crude enzyme extract. The mixture was incubated at 30°C for 30 min, and the reaction was stopped by boiling for 3 min. UDP-Glc was replaced by distilled water in the controls. The sucrose concentration was measured using the anthrone assay. SS synthesis was determined in accordance with SPS, but fructose-6-phosphate was replaced by 10 mM of fructose. Enzyme activity was expressed as $\text{ng}\cdot\text{min}^{-1}\cdot\text{g}^{-1}$ FW.

The SS cleavage activity was measured in a system of 80 mM HEPES-NaOH buffer ($\text{pH} 5.5$, 100 mM sucrose, 5 mM uridine diphosphate) and crude enzyme extract. The mixture was placed in a water bath at 30°C for 30 min, and the reaction was stopped by heating the mixture to 100°C for 3 min. The concentration of glucose generated by this reaction was determined using the DNS method. The enzyme activity was expressed as $\text{ng}\cdot\text{min}^{-1}\cdot\text{g}^{-1}$ FW.

RNA isolation and gene expression analysis. Total RNA from different peach samples was extracted using the MiniBEST Plant RNA Extraction Kit (TaKaRa, Shiga, Japan) following the manufacturer's instructions and methods previously published by Huan et al. (2016). RNase-free DNase (TaKaRa) was applied to eliminate genomic DNA. First-strand cDNA was synthesized using the PrimeScript RT Master Mix (TaKaRa) following the manufacturer's specifications. A quantitative real-time quantitative polymerase chain reaction (qPCR) was performed using the SYBR Premix Ex Taq (TaKaRa) and gene-specific primers in a $20\text{-}\mu\text{L}$ reaction volume. The qPCR was performed using a common thermo-cycling program, which included an initial denaturation at 95°C for 30 s, followed by 40 cycles of 95°C for 3 s and 60°C for 1 min. Melting curves and gel electrophoresis results were

used to confirm the specificity of the PCR. A series of dilutions of cDNA samples was used to calculate the amplification efficiency of the primers. The comparative $2^{-\Delta\Delta\text{CT}}$ method was adopted to compute the relative gene expression. Translation elongation factor 2 (TEF2) was chosen as an internal control, and cycle threshold (Ct) numbers were acquired for both the reference and target genes. All experiments were conducted in triplicate.

Statistical analyses. Statistical analyses were conducted based on triplicates for each harvest, and the concentrations of sugars, enzyme activities, and gene expressions were averaged and analyzed with an analysis of variance using GenStat (12th ed., VSN international, UK). Significant differences were determined by Tukey's least significant difference test, with the level of significance set at $P < 0.05$. Correlations between experimental variables were analyzed using Pearson's correlation coefficients.

Results

Changes in ethylene production rate and respiration intensity. The ethylene production rate of peaches gradually increased during the early storage period (days 0–4); then, it decreased during the later storage period (days 4–10) (Fig. 1A). UVC treatment significantly ($P < 0.05$) inhibited the ethylene production rate and lowered the peak concentration of ethylene, although it did not postpone the time when ethylene production peaked. At the end of the storage period (on day 10), there were no significant differences in the ethylene production rates of peaches in the CG and UVC treatment group. This indicated that UVC treatment could delay fruit ripening, especially during the early storage period.

As shown in Fig. 1B, the fruit respiration intensity of both the CG and UVC pretreatment group increased from day 0 to 6; then, it decreased during the later storage period. UVC pretreatment had no significant influence on the delay in the respiration peak, but it did inhibit the respiration rate during the later storage period (days 6–10).

There was no significant influence on firmness during the entire shelf life, indicating that fruit firmness was unaffected by UVC but that the sugar content (Table 1) was induced (Figs. 1C and 2).

Changes in concentrations of sucrose, fructose, glucose, and sorbitol. The total sugar concentration of peaches mainly consisted of sucrose, fructose, glucose, and sorbitol (Fig. 2). Among these, sucrose was the main sugar, accounting for 73.35% of the total sugar content, and the proportion of fructose to glucose was greater than 1. In both groups, sucrose concentrations (Fig. 2A) steadily decreased during the later storage period (days 4–10), but the sucrose concentration of UVC-pretreated peaches was higher than that of CG peaches ($P < 0.05$). The glucose concentration showed a gradually decreasing trend and the fructose concentration remained stable. However, UVC

Fig. 1. Effect of ultraviolet-C (UVC) pretreatment on ethylene production, respiration intensity, and firmness of peaches at 15 ± 2 °C. All values are expressed as means $\pm$ SE of three replicates. The different letters indicate significant differences at the $P < 0.05$ level (Tukey's test).

Table 1. Firmness and sugar content of yellow peach at the harvest stage.

Firmness (N)	Sucrose content (mg·g ⁻¹)	Glucose content (mg·g ⁻¹)	Fructose content (mg·g ⁻¹)	Sorbitol content (mg·g ⁻¹)
21.07 $\pm$ 0.65	54.31 $\pm$ 1.02	5.48 $\pm$ 0.21	4.71 $\pm$ 0.31	5.89 $\pm$ 0.11

treatment significantly ($P < 0.05$) increased the concentrations of fructose and glucose during the later storage period (days 6–10) (Fig. 2B and 2C). There were no significant differences in sorbitol concentrations of the peaches of the CG and UVC-treated group (Fig. 2D). In addition, the decrease in sucrose concentration in both treatment groups was accompanied by an increase in fructose and glucose concentrations during the later storage period. UVC pretreatment inhibited the degradation of sucrose and resulted in the accumulation of fructose and glucose during the later storage period. Furthermore, we found that the lower rate of ethylene production and respiration intensity, the lower the degradation rate of sucrose.

Changes in the activity of enzymes related to soluble sugar metabolism. The activity of SPS decreased but NI increased during the entire shelf life (Fig. 3). The enzyme activity of SS and AI followed the same pattern, first increasing and then decreasing. The UVC pretreatment resulted in higher SPS, AI, and NI activities from storage days 0 to 2, but it resulted in lower SS enzyme activities from

storage days 0 to 4. SPS, SS, and AI activities decreased at the end of the shelf life (days 6–10). However, the activity of NI followed the same pattern at the end of the storage period (days 4–10). UVC pretreatment significantly inhibited the decrease in SPS activity ($P < 0.05$) during the entire duration of the shelf life. During the first stage of the storage period, NI activity did not change in UVC-pretreated peaches, whereas a decreasing trend was found in control peaches. However, at the end of the storage period, the pattern was reversed, with NI activity remaining stable in the UVC-pretreated peaches and increasing in the control peaches. SS activity increased in the UVC-pretreated peaches, concomitant with the shelf life, whereas in control peaches, increases in SS activity were observed from days 0 to 4, and the SS activity was higher ($P < 0.05$) than that in the UVC-pretreated peaches. After day 4, SS activity in control peaches decreased, and SS activity was lower ($P < 0.05$) than in UVC-pretreated peaches. Inductions of AI activity were also observed in UVC-pretreated peaches on day 2 of storage. However, the peak AI activity in

CG peaches appeared on day 4 and was lower ($P < 0.05$) than the peak AI activity observed in UVC-pretreated peaches on day 2. Subsequently, the AI activity decreased on days 6–10, and AI activity was higher in UVC-pretreated peaches ($P < 0.05$) than in CG peaches.

Changes in gene expression. To understand the role of genes in sucrose metabolism, their expression profiles were measured in peaches on different shelf life days (Fig. 4). The expression of *PpaSPS1* and *PpaSPS2* showed different patterns. *PpaSPS1* expression gradually decreased during the shelf life, whereas expression of *PpaSPS2* first increased and then decreased. UVC pretreatment significantly increased the expression of *PpaSPS1* ($P < 0.05$) on day 8 and UVC pretreatment significantly increased the expression of *PpaSPS2* on day 2; subsequently, the expression levels of both genes decreased. Two members of the SS gene family were selected for expression profile analysis. The expression of *PpaSSI* in UVC-pretreated peaches was higher ($P < 0.05$) than in CG peaches on day 2, and the expression of

Fig. 2. Effect of ultraviolet-C (UVC) pretreatment on fructose (A), glucose (B), sucrose (C), and sorbitol (D) concentrations of peaches at 15 ± 2 °C. All values are expressed as means $\pm$ SE of three replicates. Different letters indicate significant differences at the $P < 0.05$ level (Tukey's test).

Fig. 3. Effect of ultraviolet-C (UVC) pretreatment on (A) sucrose phosphate synthase (SPS), (B) sucrose synthase (SS), (C) neutral invertase (NI), and (D) acid invertase (AI) activities in peaches at 15 ± 2 °C. All values are expressed as means $\pm$ SE of three replicates. The different letters indicate significant differences at the $P < 0.05$ level (Tukey's test).

Fig. 4. Effect of ultraviolet-C (UVC) treatment on expression levels of genes involved in sucrose metabolism in peaches at 15 ± 2 °C. Relative expression of each gene at harvest (day 0) is set to 1. All values are expressed as means $\pm$ SE of three replicates. The different letters indicate significant differences at the $P < 0.05$ level (Tukey's test).

PpSS2 was higher ($P < 0.05$) in UVC-pretreated peaches on days 2 and 6, whereas no significant differences ($P > 0.05$) were found between the two groups on the other days. Expression levels of *PpST1* and *PpST3* showed a similar pattern, and both decreased during the entire shelf life but were not downregulated. *PpST1* expression tended to increase and then decrease sharply to zero from days 6 to 10. Expression levels of *PpST1* and *PpST3* in UVC-pretreated peaches were significantly higher ($P < 0.05$) than in CG peaches from storage days 0 to 6. The expression level of *PpST2* was higher ($P < 0.05$) in UVC-pretreated peaches than in CG peaches only on storage day 2. The expression level of *Pppni* varied during the shelf life. There was a *Pppni* expression peak in CG peaches, but not in UVC-pretreated peaches. The expression level of *Pppni* was higher ($P < 0.05$) in UVC-pretreated peaches than in CG peaches on days 2 and 6; however, it was lower in UVC-pretreated peaches than in CG peaches on day 10.

In total, the expression levels of eight genes in CG peaches were all downregulated during the entire shelf life. This indicated that the sugar synthesis pathway was inhibited

when the CG peaches were picked from the trees and stored; consequently, the sugar synthesis rate decreased and the quality of the peaches began to deteriorate. UVC pretreatment could increase expression of some of these genes, but not all. In UVC-pretreated peaches, *PpSPS1* and *PpSPS2* were upregulated on days 8 and 2, respectively, and *PpST1* was upregulated from days 2 to 4. UVC pretreatment could accelerate the synthesis and accumulation of sucrose by upregulating the gene expression levels of *PpSPS1*, *PpSPS2*, and *PpST2* during the shelf life, which resulted in the rates of sucrose synthesis being higher than the rates of sucrose conversion. The key genes affected by UVC were *PpSPS1* and *PpSPS2*, which could maintain the sucrose content and better fruit quality. The key shelf life time points were identified as days 2 and 8.

Effects of UVC treatment on the expression of multiple genes. Compared with gene expression in CG peaches, expression levels of all genes were upregulated in UVC-pretreated peaches, with gene expression levels of up to 5 on day 2 (Table 2). Expression levels of seven, four, and three genes were upregulated on storage days 6, 8, and

10, respectively, and the numbers of genes that were upregulated decreased with the extension of the duration of the shelf life. Expression levels of two genes and one gene were downregulated on storage days 8 and 10, respectively. *PpSPS1*, *PpSPS2*, *PpST1*, *PpST2*, and *PpST3* were greatly affected by UVC pretreatment during the shelf life, and the key time points of effects of UVC pretreatment were days 2 and 6. During days 0–8, the sucrose concentration of UVC-pretreated peaches showed an upward trend, which was divided into two stages: a stage of rapid increase in sucrose concentration (days 0–2) and a stage of a steady increase in sucrose concentration (days 2–8). The sucrose concentration was significantly higher in UVC-pretreated peaches than in CG peaches. This result was consistent with the observation that expression levels of *PpSPS1* and *PpSPS2* were upregulated by UVC pretreatment, and UVC pretreatment inhibited the decrease of SPS activity. On day 10, the concentrations of glucose and fructose in UVC-pretreated peaches showed a sharp upward trend, but the sucrose concentration decreased. However, the sucrose concentration was significantly higher in UVC-pretreated

Table 2. Effect of ultraviolet-C (UVC) treatment on expressions of multiple genes in peaches.

Storage time	UVC pretreatment group and control group							
	<i>PpSPS1</i>	<i>PpSPS2</i>	<i>PpSSI</i>	<i>PpSS2</i>	<i>PpST1</i>	<i>PpST2</i>	<i>PpST3</i>	<i>Pppni</i>
Day 0	1.000 ± 0.004	1.000 ± 0.004	1.000 ± 0.004	1.000 ± 0.004	1.000 ± 0.004	1.000 ± 0.004	1.000 ± 0.004	1.000 ± 0.004
Day 2	3.506 ± 0.12	2.282 ± 0.028	6.248 ± 0.112	2.567 ± 0.098	1.927 ± 0.011	4.970 ± 0.036	5.098 ± 0.066	1.823 ± 0.002
Day 4	0.792 ± 0.001	0.901 ± 0.017	0.691 ± 0.003	0.897 ± 0.004	1.186 ± 0.001	1.686 ± 0.025	0.777 ± 0.002	0.931 ± 0.012
Day 6	3.138 ± 0.008	2.204 ± 0.064	0.933 ± 0.005	2.573 ± 0.017	2.732 ± 0.076	4.490 ± 0.104	2.324 ± 0.056	1.963 ± 0.006
Day 8	63.56 ± 8.13	1.211 ± 0.056	4.209 ± 0.062	0.942 ± 0.005	1.278 ± 0.027	0.461 ± 0.017	0.529 ± 0.091	0.859 ± 0.06
Day 10	7.127 ± 0.52	0.814 ± 0.016	0.832 ± 0.027	0.760 ± 0.032	0.573 ± 0.091	6.853 ± 0.099	2.828 ± 0.015	0.853 ± 0.021

Relative expression of each gene in control group peaches at days 0, 2, 4, 6, 8, and 10 is set to 1. All values are expressed as means ± SE of three replicates. Upregulation (fold change >1.5); downregulation (fold change <0.67).

Table 3. Correlations between the expression levels of genes involved in sucrose metabolism, enzyme activities, and concentrations of soluble sugars.

Gene	Correlation coefficients							
	Enzyme activity				Sugar content			
	SPS	SS	NI	AI	Sucrose	Glucose	Fructose	
<i>PpSPS1</i>	0.698	-0.096	-0.581	-0.209	0.360	0.619	0.902*	
<i>PpSPS2</i>	0.927**	0.460	-0.486	0.513	0.353	0.912*	0.301	
<i>PpSSI</i>	0.532	-0.881*	-0.395	-0.305	0.334	0.437	0.859*	
<i>PpSS2</i>	0.852*	-0.554	-0.451	0.224	0.299	0.802	0.571	
<i>PpST1</i>	0.669	0.027	-0.200	0.826*	-0.175	0.690	0.468	
<i>PpST2</i>	0.931**	0.428	-0.504	0.943*	0.370	0.907*	0.351	
<i>PpST3</i>	0.613	-0.199	-0.479	0.798	0.360	0.502	0.895*	
<i>Pppni</i>	0.623	0.166	0.957**	0.497	-0.194	0.674	0.208	

*, **Significant at $P < 0.05$ or 0.01 , respectively.

SPS = sucrose phosphate synthase; SS = sucrose synthase; NI = neutral invertase; AI = acid invertase.

peaches than in CG peaches. This was related to the upregulation of *PpST2* and *PpST3* gene expressions.

Relationships between gene expression, enzyme activities, and sugar concentrations. Expression levels of *PpaSPS2*, *PpaSSI*, and *PpaST3* were significantly correlated with fructose concentrations in peaches, and the expression levels of *PpaSPS2* and *PpaST2* were significantly correlated with glucose concentrations (Table 3). The enzyme activities of SPS were positively correlated with expression levels of *PpaSPS2*, *PpaSS2*, and *PpaST2*. The enzyme activities of SS, AI, and NI were positively correlated with expression levels of *PpaSSI*, *PpaST1*, and *Ppani*, respectively (Table 3). Notably, glucose and fructose concentrations were correlated with the expression levels of all genes, except *PpaSS2*, *PpaST1*, and *Ppani*. However, we did not find a correlation between sucrose concentrations and expression levels of related genes in this study. Although we did not find a correlation, SPS is an important enzyme for sucrose metabolism, and it has an important role in the development and post-harvest period of peaches.

Effects of UVC pretreatment on the ethylene production rate and respiration intensity during shelf life. Fruit respiration and ethylene production rate are major factors that contribute to senescence in postharvest fruit and involve a series of oxidation reduction reactions. Respiration converts stored sugar to energy in the presence of an oxygen substrate and ethylene induces fruit softening, thus enhancing senescence (Huan et al., 2016). Ultraviolet light (UVC) is an important alternative physical treatment (Bintsis et al., 2000) that can reduce the microbial load on fruit surfaces while addressing the desire for reducing the use of chemicals (Issa-Zacharia

et al., 2010). The efficacy of UVC is dependent on the product surface morphology and the resistance of target microorganisms against UVC light (Syamaladevi et al., 2013). Several studies reported that UVC also slowed ripening and senescence processes in fruits and vegetables (Stevens et al., 2005) by reducing the respiration rate and ethylene climacteric activity. In this study, UVC pretreatment reduced the ethylene production rate and respiration intensity of yellow peaches and did not affect the firmness; however, it induced the sucrose content. The results showed that UVC pretreatment could improve the quality of fruit but does not delay senescence, which differed from the lower respiration rates of peaches treated with UVC that resulted in lower physiological activity and moderate metabolic activity (Alique, 2005). However, our result differed from reports that UVC pretreatment increased the respiration rate of peaches after being stored for 14 and 21 d at 5 °C (Gonzalez-Aguilar et al., 2004). The inconsistent results regarding the effect of UVC pretreatment on the respiration rate and ethylene production rate in postharvest peaches are probably caused by different storage temperatures or different UVC doses used in various studies.

Effects of UVC pretreatment on the concentrations of sucrose, fructose, glucose, sorbitol, and related enzymes during shelf life. Sugar metabolism and accumulation are particularly important to fruit quality. As the dominant sugar in peach fruit, a reduction in the concentration of sucrose is always accompanied by an increase in the concentrations of glucose and fructose during the maturation stage of peaches (Vimolmangkang et al., 2016). Wang et al. (2013) demonstrated that sucrose has a more important role than glucose or fructose in protecting peaches. These sugars

may have important roles in the processes of osmoregulation, cryoprotection, and signaling in plants (Welling, 2006). In the present study, UVC pretreatment resulted in a significant accumulation of sucrose between days 2 and 8 of storage, followed by a lower concentration of fructose and glucose. UVC pretreatment inhibited the degradation of sucrose at days 8–10 of the storage period, followed by higher concentrations of fructose and glucose. Zhang et al. (2012) demonstrated that glucose and fructose concentrations followed the same pattern, not only regarding concentrations at each sampling point but also regarding the changes in concentrations throughout development of the fruit. This may be related to the fact that UVC pretreatment upregulated the expression of genes associated with sucrose synthesis. However, this also may be related to the fact that a higher ethylene production rate during the early storage period resulted in the conversion of starch to sucrose.

Effect of UVC pretreatment on the expression of multiple genes related to sugar metabolism. Concentrations of sugars were significantly affected by UVC pretreatment, which may be caused by the activities of sucrose metabolism enzymes. Among these, AI, NI, and SS cleavage regulate sucrose decomposition (Sturm and Tang, 1999), and SS synthesis and SPS are responsible for sucrose biosynthesis (Guo et al., 2002). Zanon et al. (2015) postulated that PpSUT4 has a role in sustaining cell metabolism by regulating sucrose efflux from the vacuole compartment. Yu et al. (2016) found that the increase in sucrose observed during cold storage, associated with higher SPS and lower AI activity levels, enhances the chilling tolerance observed in heat- and methyl jasmonate-treated fruit. Han et al. (2018) reported that nitrous oxide (NO)

treatment could increase the activity of SPS in peaches by enhancing the expression levels of *PpSPS1/2*. In our study, the expression level of SPS1 was downregulated in CG peaches, and this was accompanied by a decrease in SPS activity as well as a significantly reduced sucrose concentration during the entire storage period. The expression levels of *PpST1*, *PpST2*, *PpST3*, *PpSS1*, *PpSS2*, and *Pppni* were all downregulated, and there were peaks in expression levels of *PpST1* and *PpST2* on storage day 4. Furthermore, there was an AI activity peak at the same time, and the NI activity increased significantly, accompanied by a decrease in concentrations of glucose and fructose during the early shelf life. However, the decrease in sucrose concentration in CG peaches was not paired with an increase in fructose and glucose concentrations on day 10. This indicated that the accumulation of sucrose may not be related to upregulation of synthesis genes, but may be related to the downregulation of the expressions of *PpST1*, *PpST2*, and *Pppni* genes, which resulted in sucrose accumulation by inhibiting transformation. This differs from results that indicated starch is hydrolyzed rapidly and sucrose accumulation was highly positively correlated with SPS activity as peaches ripened and softened (Han et al., 2018). Expression levels of *PpSPS1* and *PpSPS2* in UVC-pretreated peaches were upregulated on days 8 and 2, respectively. UVC pretreatment also resulted in peaks in SPS activity on days 4 and 8, which resulted in the rapid accumulation of sucrose. UVC pretreatment promoted the expression and activity of AI, which stimulated the degradation of sucrose and further accelerated the reduction in the concentrations of sucrose and reduced the high concentrations of sugars in peaches. Lara et al. (2009) found that NI activity and the expression level of SS in peaches could be enhanced by hot air treatment, which could decrease sucrose concentrations and result in lower concentrations of sugars. However, in our study, UVC pretreatment resulted in a significant reduction in the activity of NI, but not NI expression, at the end of the storage period. This is in accordance with the previous viewpoint that NO treatment could effectively extend fruit life (Han et al., 2018). A similar conclusion was also obtained by Sun et al. (2011). Deng et al. (2013) confirmed that the relative expression of *MdSPS1* presented a similar trend with regard to sucrose accumulation and SPS activity, and that NI was the most vital enzyme in Golden Delicious apples, followed by AI, although a consistently lower CBAI activity level was observed during the entire storage period. However, Tong (2009) proposed a different view and suggested that AI may have an important role in sucrose metabolism and hydrolyze sucrose to reduce sugar concentration during fruit development.

Conclusions

UVC pretreatment induced the accumulation of sucrose and did not affect firmness; however, it lowered the ethylene production

and respiration rates during shelf life. The expression levels of *PpSPS2*, *PpSS1*, and *PpST3* were significantly correlated with fructose concentration, and those of *PpSPS2* and *PpST2* were significantly correlated with glucose concentration. The enzyme activity of SPS was positively correlated with *PpSPS2*, *PpSS2*, and *PpST2*. The enzyme activities of SS, AI, and NI were positively correlated with *PpSS1*, *PpST1*, and *Ppni*, respectively. Expressions of *PpSPS1* and *PpSPS2* in UVC-pretreated peaches were upregulated on storage days 8 and 2, and there was a UVC-induced peak in SPS activity on storage days 4 and 8, which resulted in the rapid accumulation of sucrose. In conclusion, UVC pretreatment could improve the quality of peaches during shelf life, which could ease the problem of lower quality and storage disorders by postharvest handling and ripening in the market, thereby increasing peach fruit consumption.

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