Running Title: UV-B increased sucrose and sorbitol contents of cultivation peach before second fruit-expansion stage.

3

Highlight: A high-sugar variety of peach ‘Lumi 1’ was used. The increased SPS, SUS, SUT and SOT promoted synthesis and intake of sugars into fruit during UVB treated.

6

Sugar metabolism changes in response to the ultraviolet B irradiation of peach (*Prunus persica* L.)

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Xuxu Wang^{1,2†}, Xiling Fu^{1,2†}, Min Chen^{1,2}, Lei Huan^{1,2}, Wenhai Liu³, Yangang Gao^{1,2}, Wei Xiao^{1,2}, Xiude Chen^{1,2}, Ling Li^{1,2*} and Dongsheng Gao^{1,2*}

¹ College of Horticulture Science and Engineering, Shandong Agricultural University, Taian 271018, China

² State Key Laboratory of Crop Biology, Shandong Agricultural University, Taian 271018, China

³ Weifang Engineering Vocational College, Weifang 261061, China

† These authors contributed equally to this work. * These authors parallel correspondence.

* Correspondence: lilingsdau@163.com; dsgao@sdau.edu.cn.

20

Abstract

The protected cultivation of peach (*Prunus persica* L.) trees is more economical and efficient than traditional cultivation, resulting in increased farmers’ incomes, but the

24 peach sugar contents are lower than in open planting. In the greenhouse, a high-sugar
 25 variety of peach ‘Lumi 1’ was irradiated with $1.44 \text{ KJ} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ intensity ultraviolet B
 26 radiation. The soluble sugar contents in fruit, peel and leaf were quantified using
 27 liquid chromatography. Overall, sucrose and sorbitol increased before the second
 28 fruit-expansion period. To further understand the mechanisms regulating sucrose and
 29 sorbitol accumulation in peach fruit, expression profiles of genes involved in sugar
 30 metabolism and transport were measured. The activity and translocation protein
 31 contents of these enzymes were measured by enzyme-linked immunosorbent assay.
 32 The increased sucrose synthase activity and sucrose transporter level in the pericarp
 33 promoted the synthesis of sucrose and intake of sucrose into fruit. Sorbitol transport
 34 into fruit was promoted by the increased sorbitol transporter protein levels in leaves.
 35 In summary, greenhouse the sucrose and sorbitol contents were increased when
 36 supplemented with $1.44 \text{ kJ} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ ultraviolet B radiation before the second
 37 fruit-expansion period of peach.

38 **Keywords:** Peach, ultraviolet B, greenhouse, sucrose, sorbitol, sugar metabolism
 39 related enzymes.

40

41 Introduction

42 The peach (*Prunus persica* L.) originated in China have been grown there for 3,000
 43 years (Zheng et al., 2014). The protected cultivation of fruit trees is more economical
 44 and efficient than traditional cultivation, resulting in increased farmers’ incomes and
 45 the economic development of rural areas (Wang et al., 2016). Therefore, the protected
 46 cultivation of fruit trees in China has increased in recent years (Wang et al., 2016).

47 However, cultivated plants are restricted by light, ultraviolet (UV) radiation,
48 ventilation and other environmental factors (Campbell et al., 2005). Thus, the
49 protected cultivation of peach trees reduces the fruits' flavor and soluble solid content
50 compared with outdoor cultivation under natural conditions (Desnoues et al., 2014;
51 Rolland et al., 2006). This seriously affected the profitability of the peach industry
52 and its sustainable development, which do not meet consumer expectations (Crisosto,
53 2002). Therefore, it is important to improve the adaptability of peach to the
54 greenhouse environment and improve the fruit quality.

55 Sweetness is an important component determine fruit quality which depends on
56 the sugar contents and composition (Kroger et al., 2006). 'Lumi 1' (*Prunus persica* L.
57 cv. Lumi 1) is a high-sugar variety with a soluble solids content of 13% . It was bred
58 in our laboratory, and is a bud mutation of 'Snow Kist', a USA peach variety. The peel
59 is dark red with white flesh, with desired hardness, adhesion, flavor and fragrance. Its
60 vitamin C content was 6.98 mg·100 g⁻¹. Thus, it has excellent qualities, as well as
61 good storage and transportation performances.

62 The photosynthetic products of rosaceae plants, such as apple (Filip et al., 2016),
63 cherry (Gao et al., 2003), loquat (Suzuki et al., 2014), peach (Bianco et al., 2000) and
64 pear (Quro et al., 2000), are transported by the main metabolites of sorbitol and
65 sucrose into the fruit (Yamaki, 2010). In higher plants, sugars are important structural
66 materials and energy sources, and they also affect growth and development
67 throughout the plant's life cycle, playing central roles in germination, flowering and
68 senescence (Loreti et al., 2001; Yao et al., 2011; Leskow et al., 2016). Sugars also
69 have signaling functions (Dekkers et al., 2004; Kato-Noguchi et al., 2010; Rolland et

70 al. 2006).

71 Important biochemical indices include the activity levels of important enzymes,
 72 which are strongly correlated to sucrose metabolism (Beruter and Studer Feusi, 1995).
 73 In peach or other Rosaceae plants, sucrose, sorbitol, glucose and fructose are mainly
 74 transported into the vacuoles by sucrose transporter (SUT), sorbitol transporter (SOT),
 75 tonoplasmic monosaccharide transporter (TMT) and sugar transporter protein (STP),
 76 which are special transporter proteins located on the vacuole membrane (Hu et al.,
 77 2014; Sauer, 2007; Büttner, 2007). The SUT mainly mediates the transport of sucrose
 78 and maltose (Sauer, 2007), and the SOT mainly mediates the transport of sorbitol (Hu
 79 et al., 2014). The TMT and STP mainly mediate the transmembrane transport of
 80 glucose, fructose and lactose (Büttner, 2007). Sucrose enters the cell as sucrose or as
 81 hexose and is first hydrolyzed into glucose and fructose by cell wall invertase
 82 (CWINV) (Persia et al., 2008), which is related to plant stress resistance (Albacete et
 83 al., 2015). In sink cells, the transported sugars are either metabolized or stored. In the
 84 cytoplasm, there are a variety of enzymes involved in sugar metabolism that form a
 85 complex regulatory network, including neutral invertase (NINV), sucrose phosphate
 86 synthase (SPS) (Hashida et al., 2016; Yativ et al., 2010) and sucrose synthase (SUS)
 87 (Klotz and Haagensohn, 2008). Vacuolar acid invertase (VAINV) can convert sucrose
 88 to fructose and glucose (Lin et al., 2015) after sucrose is transported into the vacuole
 89 (Chen et al., 2017). Sorbitol is synthesized in source tissues, such as chloroplast cells,
 90 by sorbitol-6-phosphate dehydrogenase (S6PDH) (Kim et al., 2015). In chloroplast
 91 cells, sorbitol is also hydrolyzed into hexose by sorbitol dehydrogenase (SDH).
 92 However, SDH and sorbitol oxidase (SOX) can convert sorbitol to fructose and

93 glucose after sucrose is transported into the parenchymal cells (Nosarzewski et al.,
94 2007; Yamaguchi et al., 1994). The sugar metabolism of Rosaceae plants is shown in
95 Fig. 1 (Teo et al., 2006; Wang et al., 2009).

96 UV-B regulates plant growth, development, photosynthesis, the antioxidant
97 system and endogenous hormones, and it affects the quantity of plants produced
98 (Kakani et al., 2003; Wijewardana et al., 2016; Vanhaelewyn et al., 2016). Research
99 on the postharvest quality of peaches treated with UV-B has been reported (Scattino et
100 al., 2014). However, if the greenhouse lacks light, then the fruit quality declines.
101 Although UV-B radiation acts as an environmental stimulus, in high doses it has
102 detrimental effects on plant metabolism (Trentin et al., 2015). In our experiments
103 peaches were treated with UV-B radiation during the fruiting period in 2015, and the
104 results showed that supplementation with $1.44 \text{ kJ} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ of UV-B radiation can
105 significantly improve the sugar content of peach fruit grown in a greenhouse. Based
106 on this, little information is available in the literature on the effects of UV-B radiation
107 on the sugar metabolism-related enzymes in a new peach variety Lumi 1. Knowledge
108 of the control of sugar metabolism is essential to enhance fruit quality and promote
109 fruit consumption (Desnoues et al., 2016). We investigated the changes in sugar
110 accumulation and sugar metabolism-related enzymes when $1.44 \text{ kJ} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ UV-B
111 intensity irradiated of peach trees, Lumi 1. There has been limited research on the
112 effects of UV-B radiation on sugar metabolism in peach, thus our research has laid a
113 foundation for future research.

114

115 **Materials and methods**

116 *Plant material*

117 The five-year-old peach trees (*P. persica* L. cv. Tainongtianmi) and four-year-old
118 peach trees (*P. persica* L. cv. Lumi 1) were harvested from the same experimental and
119 professional plantations located in an automated polycarbonate-covered greenhouse at
120 the horticultural science experimental station of shandong agriculture university,
121 located in Tai'an, China (117°06' E, 36°15' N).

122

123 *UV-B treatment*

124 Screening for the optimum UV-B radiation dose. The using UV-B lamp tubes (30W,
125 297nm; Nanjing Huaqiang Electronics Co., Ltd., China), the UV-B irradiation was
126 carried out by treatments of $0.72 \text{ kJ} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$, $1.44 \text{ kJ} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ and $2.16 \text{ kJ} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ from
127 February 2015 to May 2015. The control supplemental UV-B dose was $0 \text{ kJ} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$.
128 The UV-B lamp tube were hang at 0.9 m from the top of the plant. UV-B radiation
129 doses were controlled using an electronic automatic device, from flowering to fruit
130 maturity one hour every day from 10 a.m. to 11:00 a.m.. This program will be
131 suspended when it was cloudy, raining or snowing. The water-fertilizer conditions of
132 treatment group and control group were the same.

133 The changes in sugar accumulation and sugar metabolism-related enzymes in
134 'Lumi 1' were investigated under UV-B radiation. UV-B radiation treatments were
135 carried out at $1.44 \text{ kJ} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ from February 2016 to May 2016 and supplemental
136 UV-B radiation dose was $1.44 \text{ kJ} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ with supplemental $0 \text{ kJ} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ UV-B dose
137 as control, and all other conditions being the same with screening for the optimum
138 UV-B radiation dose.

139 Peach fruits and leaves around fruit were sampled every 14 days from the first
140 fruit-expansion stage to the maturation stage, as Table 1 shown. The sarcocarp,
141 pericarp and leaf samples were immediately frozen in liquid nitrogen and then stored
142 at -75°C for later use.

143

144 *Fresh and dry weight measurements*

145 Ten peach fruits were randomly sampled and weighed, then kiln dried, and the water
146 content was calculated.

147

148 *Total anthocyanin extraction and measurement*

149 Anthocyanins were extracted from fresh peach sarcocarp and pericarp in 95% ethanol
150 (pH2) and measured spectrophotometrically at 530 nm, 620 nm and 650 nm. The
151 anthocyanin content was calculated using the following equations:

152 $D_{\lambda} = (A_{530} - A_{620}) - 0.1(A_{650} - A_{620})$ and

153 Anthocyanins content ($\text{mg} \cdot \text{g}^{-1}$) = $\frac{OD_{\lambda}}{\xi_{\lambda}} \times \frac{V}{W} \times 106$,

154 where ξ_{λ} (Anthocyanin molecule's 530 nm light extinction coefficient) = 4.62×10^4 ,

155 V indicates the total volume of the extract; W indicates the sample weight (g FW:

156 Fresh weight); and 106 is the number of molecules of mg in mg .

157

158 *Chlorophyll and carotenoid extractions and measurements*

159 Chlorophyll and carotenoid were extracted from fresh pulp, peel and leaf in 96%
160 ethanol and measured spectrophotometrically at 665 nm, 649 nm and 470 nm. The

161 chlorophyll and carotenoid contents were calculated using the following equations:

162 $Ca = 13.95 D_{665} - 6.88 D_{649};$

163 $Cb = 24.96 D_{649} - 7.32 D_{665};$

164 $Cx \cdot c = \frac{1000 D_{470} - 2.05 Ca - 114.8 Cb}{245};$ and

165 $\text{Pigment content} = \frac{Ca (Cb, Cx \cdot c) \times V \times \frac{n}{W}},$

166 where Ca represents the concentration of chlorophylla; Cb represents the
167 concentration of chlorophyllb; Cx·c represents the concentration of carotenoid; V
168 indicates total volume of extract; W indicates the sample weight (g FW); and n
169 indicates the dilution factor.

170

171 *Total phenolics and phenolic components extractions and measurements*

172 Peach sarcocarp and pericarp were used in extractions under the following conditions
173 previously selected (Liu et al., 2015) with slight modifications. Samples were
174 extracted in acidic methanol-water (50:50, v/v, pH 2). Then, they were extracted in
175 70% aqueous acetone. Phenolic compounds that were extracted were stored at −20°C
176 until being used in the next 24 h. The Folin–Ciocalteu method was used to determine
177 the total phenolic content of the extracts (Singleton and Rossi, 1964). Each treatment
178 consisted of three biological replicates, and each sample was measured using three
179 technical replicates. The data from a typical experiment are presented.

180 High-performance liquid chromatography (HPLC) was used for the identification
181 and quantification of mature phenolic components of peach sarcocarp and pericarp in
182 a Waters series 600 chromatography unit (HPLC; Waters, Milford, MA, USA)

183 equipped with two 515 pumps and a 2487 dual UV detector (Waters Alliance 2695
184 HPLC) at a wavelength of 280 nm. The chromatographic separation of phenolic
185 components was carried out using eluent A, acetic acid aqueous solution (pH 2.8), and
186 eluent B, acetonitrile, as the mobile phase, with a flow rate of 1.0 mL per min.
187 Samples were injected onto a Kromasil C18 (250 × 4.6 mm) column, and the gradient
188 was programmed as follows: 90–65% B (0–30 min), 65% B (30–40 min), 65–90% B
189 (40–42 min) and 90% B (42–45 min). Operating conditions were as follows: column
190 temperature was 35°C; injection volume was 10 µL, and the sensitivity was 0.5 aufs.
191 Each treatment consisted of three biological replicates, and each sample was
192 measured using two technical replicates. Data from a typical experiment are
193 presented.

194

195 *Sugar and organic acid compound extractions and measurements*

196 Samples were extracted from fresh pulp, peel and leaf in 85% ethanol and then dried.
197 Dry solids were reconstituted in 2 mL of deionized water, and measured by HPLC for
198 identification (Liu et al., 2015).

199 The chromatographic separation of sugars of pulp, peel and leaf were
200 implemented using acetonitrile–water (75:25, v/v) as the mobile phase with a flow
201 rate of 0.8 mL per min and a 5.0 µm NH₂ (4.6 mm×250 mm) column (GL Sciences
202 Inc., Torrance, CA, USA). The samples' chromatographic separations were performed
203 on an YMC-Pack Polyamine II (4.6 mm×250 mm) column. Eluted peaks were
204 detected with an RID-10A refractive index detector (Shimadzu Co., Kyoto, Japan).
205 Operating conditions were as follows: column temperature was 30°C, injection

206 volume was 10 μ L and the sensitivity was 4 aufs.

207 Organic acid analyses of pulp were carried using a Waters series 515
208 chromatography unit (HPLC) equipped with two 515 pumps and a 2487 dual UV
209 detector at a wavelength of 210 nm. The chromatographic separation of organic acids
210 was carried out using $\text{NH}_4\text{H}_2\text{PO}_4$ (10 mmol/L, pH 2.3) and methanol (98:2, v/v) as the
211 mobile phase, with a flow rate of 0.8 mL per min, and samples were injected onto a
212 Thermo Hypersil GOLD aQ (4.6 mm $\times$ 250 mm) column. Operating conditions were as
213 follows: column temperature was 28°C, injection volume was 10 μ L, and the
214 sensitivity was 0.5 aufs.

215

216 *Sample extraction and enzyme-linked immunosorbent assay (ELISA)* 217 *measurements*

218 Samples of peach sarcocarp and leaves were extracted in phosphate buffered saline
219 (pH 7.4; TransGen Biotech, Beijing, China) (1:9, m/v) and fully homogenized.
220 Enzyme liquid was stored at -20°C for no more than 7 days before being used.

221 Sugar metabolism-related enzyme activities, including SUS, SPS, CWINV,
222 NINV and VAINV, and S6PDH, SDH, SOX and SOT of sorbitol metabolism-related
223 enzyme activities, were quantified by a Plant ELISA Kit (Dong Song Bo Industry
224 Biotechnology Co., LTD, Beijing, China), following the manufacturer's protocol.
225 Additionally, the same methods were used to measure the sugar transporter-related
226 protein contents, including SUT, STP and TMT.

227 Pectinase activity was determined by ELISA method same as sugar
228 metabolism-related enzyme.

229

230 *Gene identification and primer design*

231 The sugar metabolism-related genes investigated, *PpSUS*, *PpSPS*, *PpCWINV*,
232 *PpNINV* and *PpVAINV*, and the sugar transporter genes investigated, *PpSUT*, *PpSTP*
233 and *PpTMT*, were identified in Vimolmangkang et al. (2015). The sorbitol
234 metabolism-related genes investigated, *PpS6PDH* and *PpSDH*, were identified in the
235 NCBI database. We searched the peach genome's annotated database to identify sugar
236 metabolism-related genes (Verde et al., 2013). The coding sequences of these genes
237 were further compared against the peach draft genome using the BlastN algorithm,
238 and the genome sequences of sugar metabolism-related genes in peach were
239 downloaded from *P. persica* v2.1 of the Phytozome database (<https://phytozome.jgi.doe.gov/pz/portal.html>). Primer 3 (<http://bioinfo.ut.ee/primer3-0.4.0/>) was used
240 for primer design. Primer sequences for this study are shown in Table S1.

242

243 *RNA isolation and qRT-PCR analyses*

244 Total RNA was extracted from 500 mg of sarcocarp, pericarp and leaves using an
245 RNeasy Pure Plant Kit (Polysaccharides & Polyphenolics-rich; Tiangen, Beijing,
246 China). The single-stranded cDNAs were synthesized from 1 µL of RNA using a
247 Prime Script RT reagent kit with gDNA Eraser (Takara, Dalian, China). The qRT-PCR
248 was performed with a gene-specific primer pair, and the peach gene *GADPH* as an
249 internal control (Tong et al., 2009). Reactions were performed on a CFX96 real-time
250 PCR detection system with SYBR Premix Ex Taq (Takara) following the
251 manufacturer's instructions. The thermo-cycling parameters were as follows: 30 s at

252 95°C, followed by 40 cycles of 10 s at 95°C for denaturation and 40 s at 60°C for
253 annealing and extension (Vimolmangkang et al., 2015). The specificity of the PCR
254 was assessed by the presence of a single peak in the dissociation curve after the
255 amplification and by the size estimation of the amplified product. The comparative
256 cycle threshold (CT) method ($2^{-\Delta\Delta CT}$) method was used to quantify cDNAs with
257 amplification efficiencies equivalent to that of the reference actin gene (Graeber et al.,
258 2011). Each experiment was repeated at least three times using the same cDNA
259 source.

260 The fluorescence quantitative CT values of *PpCWINV1,2,3,6*, *PpNINV5,6* and
261 *PpTMT3,4* from leaf, pericarp and fruit were greater than 35; therefore, we assumed
262 that they were not expressed in the tested peach variety.

263

264 *Statistical analyses*

265 All assays were conducted with three or more biological replicates. The statistical
266 analysis was performed using SPSS for Windows version 19 (SPSS) (Chicago, IL,
267 USA). Categorical variables were expressed as frequencies, and percentages and
268 continuous variables were expressed as means $\pm$ SEs, as appropriate. The data were
269 analyzed by an analysis of variance and, when appropriate, Duncan's test was used. A
270 significance level of $P < 0.05$ was applied.

271

272 **Results**

273

274 *1.44 kJ·m⁻²·d⁻¹ UV-B radiation increased the sugar content and decreased the*

275 *acid content*

276 1.44 kJ·m⁻²·d⁻¹ UV-B radiation was the most effective in increasing the sugar content
277 and reducing the acid content of the peach variety ‘Tainongtiamnmi’ in the three
278 UV-B radiation intensities used in this study (Fig. 2). Its total sugar content was 1.5
279 times as much as that of the control.

280

281 *Quality and appearance of ‘Lumi 1’ during the UV-B treatment*

282 The 1.44 kJ·m⁻²·d⁻¹ UV-B radiation did not produce obvious effects on fresh weight,
283 dry weight or the water content of the peach fruit (Fig. S1). Pectinase can reflect fruit
284 softening (Santiago-Doménech et al., 2008). Pectinase activity was first increased by
285 UV-B treatment, then decreased activity in the mature period compared with the
286 control (Fig. S2).

287 The fruit color of sarcocarp and pericarp were significantly enhanced after UV-B
288 treatment during the ripening stage (Fig. 3A, 3B). The anthocyanin contents in flesh
289 and peel were significantly elevated compared with those in the control (Fig. 3C, 3D).
290 After treatment with UV-B, there was no obvious law of change in the chlorophyll
291 content, which was mainly increased in the flesh, but decreased in the pericarp and
292 leaf (Fig. S3). The levels of carotenoids in the flesh, peel and leaf were mainly
293 decreased by UV-B (Fig. S3).

294 Under UV-B radiation total phenolics content in the flesh was mainly increased
295 (Fig. S4A). In the pericarp total phenolics content did not significantly change
296 compared with in the control (Fig. S4B). At the mature stage, only the protocatechuic
297 acid content was greater than in the control of sarcocarp, while in the pericarp, only

298 the neo-chlorogenic acid content was greater than in the control (Fig. S4C).

299 *Change in sugar content during UV-B treatment of 'Lumi 1'*

300 After UV-B treatments, the total sucrose and sugar content levels increased compared
301 with those of the control at the first fruit-expansion and slow-growth stages in
302 sarcocarp (Fig. 4A). Consistently, the sugar-acid ratio was twice as much as control at
303 late of slow-growth stage stage (Fig. 4B). Fructose and glucose in pulp were not
304 significantly changed (Fig. 4C). The organic acid components and total organic acid
305 content were decreased by UV-B at the slow growth phase (Fig. S5).

306 During UV-B treatment the changes in the sucrose and total sugar contents in
307 peel were not significant (Fig. 4D). The sucrose and total sugar contents in leaf
308 mainly decreased, but the changes were not significant (Fig. 4E). The fructose and
309 glucose contents in the pericarp and leaf were mainly reduced by UV-B (Fig. S6).

310 Thus, the effects on sucrose metabolism were divided into two stages, before the
311 second fruit-expansion stage and after the slow growth period.

312

313 *Changes in sucrose metabolism and transport before the second* 314 *fruit-expansion stage*

315 The peach pulp is part of the sink tissue, therefore, the sucrose in the pulp cell was
316 decomposed into fructose and glucose by SUS, SPS and INV (Fig. 1). Under UV-B
317 treatment the SPS enzyme activity increased was up-regulated by *PpSPS2* and
318 *PpSPS4* gene expression levels before the second fruit-expansion stage (Fig. 5A).
319 Under regulation of four *PpSUS* genes the SUS activity was first raised and then
320 decreased (Fig. 5B). *PpCWINV4* and *PpCWINV5* gene expression levels were

321 decreased, but there were no significant declines in CWINV enzyme activity (Fig. 5C).
 322 Expressions of two *PpVAINV* genes were increased, consistently, VAINV activity was
 323 rised compared with the control (Fig. 5D). Expression levels of six *PpNINV* genes
 324 were down-regulated by UV-B; therefore, the NINV activity was decreased (Fig. 5E).
 325 SUT content and the *PpSUT* genes' expression levels were decreased by UV-B
 326 compared with the control (Fig. 6A). STP's protein content was first increased, and
 327 then decreased under the regulation of two *PpSTP* genes (Fig. 6B). TMT protein
 328 content was decreased by UV-B, by two *PpTMT* genes regulation (Fig. 6C).

329 SPS activity was first increased and then decreased under the regulation of four
 330 *PpSPS* genes of pericarp during UV-B treatment (Fig. 7A). SUS activity was
 331 significantly higher than in the control under the regulation of four *PpSUS* genes (Fig.
 332 7B). Additionally, the SUT protein contents in the first two periods was significantly
 333 increased compared with the control under the regulation of three *PpSUT* genes, and
 334 then it decreased during the late of slow-growth stage period (Fig. 7C). The enzyme
 335 activities of CWINV, VAINV and NINV, the protein content levels of STP and TMT,
 336 and their gene expression levels were significantly increased by UV-B radiation (Fig.
 337 S7).

338 SUS and NINV enzyme activities and their gene expression levels were mainly
 339 increased of leaves during the UV-B treatment, while SPS, CWINV and VAINV
 340 enzymes and their gene expression levels did not change significantly (Fig. S8). SUT
 341 protein level first increased and then decreased, which was contrary to the
 342 accumulation of sugar in the flesh (Fig. S9A). STP and TMT protein and gene
 343 expression levels were increased compared with the control (Fig. S9B,9C).

344 In general, the fruit sugar content increased before the second fruit-expansion
345 stage due to the increased synthesis and transport of sucrose in pericarp and inhibition
346 of sucrose decomposition and transport in sarcocarp. It had little correlation with the
347 synthesis and translocation of sugars in leaf.

348

349 *Changes in sucrose metabolism and transport after the slow-growth period*

350 In sarcocarp, SPS, SUS, CWINV and NINV activities were gradually decreased
351 during UV-B treatment, which were regulated by *PpSPS*, *PpSUS*, *PpCWINV* and
352 *PpNINV* expression levels, the VAINV activity was increased compared with that of
353 the control after the slow-growth period (Fig. 8). The levels of SUT, STP and TMT
354 proteins and their gene expression levels in pulp were decreased by UV-B (Fig. 9).

355 In pericarp, the SPS and SUS activities were decreased regulated by four *PpSPS*
356 and four *PpSUS* gene expression during UV-B treatment (Fig. 10A, 10B). SUT level
357 and three *PpSUT* expression levels were also decreased (Fig. 10C). CWINV activity
358 and gene expression were decreased by UV-B radiation. VAINV activity, and STP and
359 TMT levels and their gene expression levels, were increased. Changes in NINV
360 activity were not observed (Fig. S10).

361 In leaf, regulated by *PpSPS* expression the SPS activity gradually decreased.
362 SUS, CWINV and NINV activities and their gene expression levels were decreased
363 by UV-B treatment. Only VAINV's activity and *PpVAINV*'s expression level were
364 increased during UV-B treatment (Fig. S11). The transport of sugars, SUT's protein
365 level and the *PpSUT* expression level were decreased by UV-B radiation, while STP
366 and TMT protein levels, and *PpSTP* and *PpTMT* gene expression levels were

367 increased (Fig. S12).

368 On the whole, sugar decreased in fruit after the slow-growth period, which was
369 cause by the inhibition of sucrose decomposition and transport in pericarp and leaf.

370

371 *UV-B radiation increased the sorbitol content of fruit*

372 During the UV-B treatment, in the late of slow-growth stage and mature stages, the
373 sorbitol content in fruit was significantly higher than in the control (Fig. 11A).

374 Compared with the control, sorbitol content in the peel and leaf was first decreased
375 and then increased, the changes were not significant (Fig. 11B, 11C).

376 In sarcocarp, SDH activity and *PpSDH* expression were first decreased and then
377 increased compared with in the control (Fig. 12A). The SDH activity of pericarp was

378 only significantly greater than the control at the early of slow-growth stage. Its
379 enzymatic activity were decreased in the first fruit-expansion and mature stages

380 compared with in the control. However, the enzymatic activity was increased in the
381 other periods, under the regulation of *PpSDH* (Fig. 12B). In leaf, SDH activity was

382 lower than in the control at the mature stage, but this did not correlate with the
383 expression levels of *PpSDH* (Fig. 12C). The sorbitol content was inversely

384 proportional to the SDH activity in sarcocarp, pericarp and leaf. In leaves, the SOT
385 level was greater than in the control, facilitated by the transport of sorbitol to sink

386 fruits (Fig. 13). S6PDH and SOX activities and the sorbitol content were not clearly
387 regulated (Fig. S13).

388

389 Discussion

390 *UV-B and fruit quality*

391 Recently, greenhouse peach consumption has been declining because of the fruit's
 392 poor flavor, which falls short of consumer expectations (Crisosto, 2002). UV-B
 393 radiation slows grape berry development and up-regulates flavonol and anthocyanin
 394 biosynthesis (Martínez-Lüscher et al., 2014). Consistently, after UV-B treatment
 395 anthocyanin contents of ripe peach fruits' were increased in pulp and peel, with the
 396 mature fruit coloring phenotype was deepened. However, no effects of the total
 397 phenol content were observed during UV-B treatment. In peach fruit, the tendency of
 398 sugar levels is to first increase and then decrease (Vizzotto et al., 1996), identical,
 399 trends of sugar content in sarcocarp were not altered after UV-B radiation. After UV-B
 400 radiation supplemented with nitrogen, phosphorus and potassium, the soluble sugars
 401 of pea plants are significantly enhanced (Singh et al., 2015). UV-B alleviates the
 402 uncoupling effects of elevated CO₂ and increased temperature, which modulates the
 403 accumulation of sugars and upregulates the anthocyanin biosynthesis of grape berry
 404 (Martínez-Lüscher et al., 2016). Unlike the sugar results in 'Tainongtianmi', the sugar
 405 content after 1.44 kJ·m⁻²·d⁻¹ UV-B radiation was significantly enhanced, the sugar
 406 content in this experiment of 'Lumi 1' was slightly lower than in the control at
 407 maturity, which may have resulted from the different peach varieties used.
 408 High-intensity UV-B irradiation reduces the photosynthetic capacities of plants,
 409 resulting in crop plants becoming shorter, and having lower yields and chlorophyll
 410 contents, as well as undergoing photosystem II damage and a change in the carbon
 411 partitioning in plant organs (Schumaker et al., 1997; Feng et al., 2003; Zhang et al.,
 412 2016). The sugars may have been reduced because of long-term UV-B radiation of

413 peach fruit at after slow-growth stage.

414

415 *UV-B, sucrose metabolism and translocation*

416 The Rosaceae plants' sugar metabolism is shown in Fig. 1. In the source leaf,
 417 first there is the photosynthetic synthesis of glucose-6-phosphate, then SPS and SUS
 418 catalyze the synthesis of sucrose, which is decomposed into hexose under the
 419 catalysis of the INV. Sucrose and hexose are transported to sink fruit under the action
 420 of sugar transporters. In the sink fruit, sucrose is decomposed into fructose and
 421 glucose by the catalysis of SPS, SUS and INV (Teo et al., 2006; Wang et al., 2009).
 422 UV-B treatment at gene expression and biochemical levels had different effects on
 423 these carbohydrate-metabolizing enzymes in flesh, peel and leaf. Previous studies on
 424 sugar-metabolism showed that coordinated interactions among SUS, SPS and NINV
 425 were related to sucrose metabolism and accumulation in the cytosol (Vimolmangkang
 426 et al., 2015). In rice, *PpSUT2* is involved in sucrose transport across the tonoplast
 427 from the vacuole lumen to the cytosol, playing an essential role in sugar export from
 428 the source leaves to sink organs (Eom et al., 2011). *PpSUTs* are related to sucrose
 429 metabolism and accumulation in the cytosol, participate in phloem loading in leaves
 430 and are involved in sucrose accumulation in peach fruit (Zanon et al., 2014). During
 431 UV-B treatment the increased SUT protein levels was up-regulation by *PpSUTs* of
 432 peel. The *PpSTP* gene encodes a monosaccharide transporter (Fotopoulos et al., 2003),
 433 and the heterologous expression of *PpSTP1* in yeast revealed that the encoded protein
 434 catalyzes the high-affinity uptake of glucose, galactose and mannose (Rottmann et al.,
 435 2016). TMT is well-known as a vacuolar monosaccharide importer (Wormit et al.,

2006). During UV-B treatment, the decreases in SUT, STP and TMT inhibited the sucrose transport from leaves and pericarp to the fruit after the slow-growth period after the slow-growth period. Therefore, the fruit sugar content increased before the second fruit-expansion stage due to the increased synthesis and transport of sucrose in pericarp and inhibition of sucrose decomposition and transport in sarcocarp. It had little correlation with the synthesis and translocation of sugars in leaf before second fruit-expansion stage of peach fruit development. Sugars were decreased in fruit after the slow-growth period, caused by the inhibition of sucrose decomposition and transport in pericarp and leaf. This may have been caused by sink-source relationships in fruit trees, in which, at the early stages of fruit development, the competition for nutrients is greater than in mature fruits (Lenz, 1979).

447

448 *UV-B, sorbitol metabolism and translocation*

Sorbitol is mainly accumulated in source leaves in peach, and it constitutes up to 80% of the total solutes involved in osmotic adjustment (Bianco et al., 2000). Sorbitol is found mainly in leaves. In Rosaceae fruit trees, such as apple, pear and peach, leaf disc experiments showed enhanced sorbitol accumulation under salt, osmotic and low-temperature stresses, and ABA-mediated S6PDH plays a role in sorbitol biosynthesis in various stress responses (Kanayama et al., 2007). SDH exhibits the highest activity on oxidized sorbitol (Aquayo et al., 2013; Jia et al., 2015). Yeast transformed with the *MdSOTs* of apple had a significant sorbitol up-take (Watari et al., 2004). During UV-B treatment, the changes in the sorbitol content were opposite to those in the SDH activity in sarcocarp, peel and leaf. The SDH activity increased

when the sorbitol content decreased, identically SDH activity decreased when the sorbitol content increased. However, SDH activity was increased and the content of sorbitol did not decrease may be due to the increased SOT protein level in the leaves, which accelerated the transport of sorbitol to the fruit during the UV-B treatment after slow-growth stage of fruit development.

UV-B and plant stress resistance

Under salt stress, *TMT2* was observed to increase in abundance (Pertlobermeyer et al., 2016). Oxalic acid can significantly enhance the SUS cleavage function and SOX activity, while it also increases the sugar (glucose and fructose) content (Wang et al., 2016). Sucrose and sorbitol content were increased due to the *PpTMT* expression levels and SUS and SOX activities increased in some periods of fruit development after UV-B treatment in this experiment. Therefore, we speculate that UV-B treatment may improve the resistance of peach trees but this requires further experimental verification. Greenhouse experiments have numerous limiting factors, but in the future studies under UV-B conditions, we will add other external factors, such as CO₂ or nitrogen, phosphorus and potassium, to further improve the fruit quality of peaches grown in greenhouses. Related transcription factors that promote *PpSPS*, *PpSUS*, *PpSUT* and *PpSOT* genes expression during UVB treatment of peach need to be determined (Fig. 14). We hypothesize that the application in agricultural production under greenhouse conditions of 1.44 kJ·m⁻²·d⁻¹ UV-B radiation to peach before the second fruit-expansion period can increase the soluble sugar content but not the organic acids content.

482 **Supplementary data**

483 **Supplementary Table S1.** List of primers used in this study.

484 **Supplementary Fig. S1.** Effects of UV-B on fruit weight and water content.

485 **Supplementary Fig. S2.** Effects of UV-B on the pectinase activity of sarcocarp.

486 **Supplementary Fig. S3.** Effects of UV-B on chlorophyll and carotenoid contents.

487 **Supplementary Fig. S4.** Effects of UV-B on phenolic acids and the total phenolic
488 contents in the mature stage of peach development.

489 **Supplementary Fig. S5.** Effects of UV-B on organic acids.

490 **Supplementary Fig. S6.** Effects of UV-B on the fructose and glucose contents of
491 pericarp and leaf.

492 **Supplementary Fig. S7.** Effects of UV-B on INV, STP and TMT before the second
493 fruit-expansion stage in pericarp.

494 **Supplementary Fig. S8.** Effects of UV-B on sucrose metabolizing enzymes in leaf
495 before the second fruit-expansion stage.

496 **Supplementary Fig. S9.** Effects of UV-B on sugar transporters in leaf before the
497 second fruit-expansion stage.

498 **Supplementary Fig. S10.** Effects of UV-B on INV, STP and TMT after the
499 slow-growth period in pericarp.

500 **Supplementary Fig. S11.** Effects of UV-B on sucrose metabolizing enzymes in leaf
501 after the slow-growth period.

502 **Supplementary Fig. S12.** Effects of UV-B on sugar transporters in leaf after the
503 slow-growth period.

504 **Supplementary Fig. S13.** Effects of UV-B on S6PDH and SOX changes in sarcocarp,

505 pericarp and leaf.

506

507 **Conflict of interest statement**

508 The authors declare that the research was conducted in the absence of any commercial
509 or financial relationships that could be construed as a potential conflict of interest.

510

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515

516 **Author contributions**

517 XW and XL performed the experiments and wrote the manuscript. The others
518 provided technical support and theoretical support. LL and DG supervised the project.

519

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 741

742 **Table and figures title**

743 **Table 1.** Sample collection times

Sampling time	Days post-anthesis/d	Mature period
11-Mar	21	First fruit-expansion stage
25-Mar	35	early of slow-growth stage
8-Apr	49	late of slow-growth stage stage
22-Apr	63	Second fruit-expansion stage
6-May	77	Maturity stage

744 **Fig. 1.** Sugar metabolic pathway of rosaceous plants. G6P, glucose-6-phosphate; S6PDH,
 745 glucitol-6-phosphate dehydrogenase; S6P, sucrose-6-phosphate; Sor, sorbitol; SUS, sucrose
 746 synthase; SPS, sucrose phosphate synthase; Suc, sucrose; Fru, fructose; Glu, glucose; Hex,
 747 hexose; SDH, sorbitol dehydrogenase; NINV, neutral invertase; VAINV, vacuolar acid
 748 invertase; CWINV, cell wall invertase; INV, invertase.

749 **Fig. 2.** Effects of different UV-B radiation intensities on the total sugar content in
 750 peach (cv. Tainongtianmi) fruit. (A) Changes in the total sugar content after three
 751 different intensities of UV-B radiation. (B) Changes in the titratable acid content after
 752 three different intensities of UV-B radiation.

753 **Fig. 3.** Effects of UV-B treatment on the anthocyanin contents of flesh and peel, and
754 the mature fruit phenotype. (A) Peach fruit phenotype of control. (B) Peach fruit
755 phenotype after UV-B treatment. (C) Changes in the anthocyanin content in fruit flesh
756 affected by UV-B radiation (*P < 0.05). (D) Changes in the anthocyanin content in
757 fruit peel affected by UV-B radiation (*P < 0.05).

758 **Fig. 4.** Effects of UV-B on the sugar content in different peach tissues. (A) Sucrose
759 and total sugar contents in sarcocarp (*P < 0.05). (B) Sugar-acid ratio in sarcocarp (*P
760 < 0.05). (C) Fructose and glucose contents in sarcocarp (*P < 0.05). (D) Sucrose and
761 total sugar contents in pericarp (*P < 0.05). (E) Sucrose and total sugar contents in
762 leaf (*P < 0.05).

763 **Fig. 5.** Effects of UV-B treatment on sucrose metabolism enzymes in sarcocarp before
764 the second fruit-expansion stage. (A) SPS activity and gene expression levels (*P
765 < 0.05). (B) SUS activity and gene expression levels (*P < 0.05). (C) CWINV activity
766 and gene expression levels (*P < 0.05). (D) VAINV activity and gene expression
767 levels (*P < 0.05). (E) NINV activity and gene expression levels (*P < 0.05).

768 **Fig. 6.** Effects of UV-B treatment on the sugar transporter before the second
769 fruit-expansion stage in sarcocarp. (A) SUT activity and gene expression levels (*P <
770 0.05). (B) STP activity and gene expression levels (*P < 0.05). (C) TMT activity and
771 gene expression levels (*P < 0.05).

772 **Fig. 7.** Effects of UV-B treatment on SPS, SUS and SUT activity before the second
773 fruit-expansion stages in pericarp. (A) SPS activity and gene expression levels (*P <
774 0.05). (B) SUS activity and gene expression levels (*P < 0.05). (C) SUT activity and
775 gene expression levels (*P < 0.05).

776 **Fig. 8.** Effects of UV-B radiation on sucrose metabolism enzymes after the slow
777 growth period in sarcocarp. (A) SPS activity and gene expression levels (*P < 0.05).
778 (B) SUS activity and *PpSUSs* expression levels (*P < 0.05). (C) CWINV activity and
779 gene expression levels (*P < 0.05). (D) VAINV activity and gene expression levels
780 (*P < 0.05). (E) NINV activity and gene expression levels (*P < 0.05).

781 **Fig. 9.** Effects of UV-B radiation on sugar transporters after the slow growth period in
782 sarcocarp. (A) SUT activity and gene expression levels (*P < 0.05). (B) STP activity
783 and gene expression levels (*P < 0.05). (C) TMT activity and gene expression levels
784 (*P < 0.05).

785 **Fig. 10.** Effects of UV-B radiation on SPS, SUS and SUT after the slow-growth
786 period in pericarp. (A) SPS activity and gene expression levels (*P < 0.05). (B) SUS
787 activity and gene expression levels (*P < 0.05). (C) SUT activity and gene expression
788 levels (*P < 0.05).

789 **Fig. 11.** Effects of UV-B radiation on the sorbitol contents. (A) Changes in the
790 sorbitol content of sarcocarp (*P < 0.05). (B) Changes in the sorbitol content of
791 pericarp (*P < 0.05). (C) Changes in the sorbitol content of leaf (*P < 0.05).

792 **Fig. 12.** Effects of UV-B radiation on SDH activity and *PpSDH* expression levels. (A)
793 SDH and *PpSDH* in sarcocarp (*P < 0.05). (B) SDH and *PpSDH* in pericarp (*P <
794 0.05). (C) SDH and *PpSDH* in leaf (*P < 0.05).

795 **Fig. 13.** Effects of UV-B radiation on SOT activity levels. (A) SOT in sarcocarp (*P <
796 0.05). (B) SOT in pericarp (*P < 0.05). (C) SOT in leaf (*P < 0.05).

797 **Fig. 14.** Model for the sugar metabolic pathway of peach during UV-B treatment.

798 A. Sugar metabolic pathway of peach leaves. B. Sugar metabolic pathway of peach

799 sarcocarp. C. Sugar metabolic pathway of peach pericarp. The definition of
800 professional term abbreviation is the same as that of Fig. 1. In the box indicates that
801 the indicator increased during treated with UV-B. The question mark represents what
802 we need to further determine which transcription factor is regulates the protein under
803 UV-B treatment.

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Fig. 1.

835 **Fig. 2.**

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848 **Fig. 3.**

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863 **Fig. 4.**

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872 **Fig. 5.**

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876 **Fig. 6.**

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897 **Fig. 8.**

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Fig. 9.

Fig. 10.

Fig. 11.

Fig. 12.

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968 **Fig. 14.**

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