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

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.

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

Xuxu Wang[1, 2†], Xiling Fu[1, 2†], Min Chen[1, 2], Lei Huan[1, 2], Wenhai Liu[3], 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.

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

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

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

Introduction

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

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

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

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

al. 2006).

Important biochemical indices include the activity levels of important enzymes, which are strongly correlated to sucrose metabolism (Beruter and Studer Feusi, 1995). In peach or other Rosaceae plants, sucrose, sorbitol, glucose and fructose are mainly transported into the vacuoles by sucrose transporter (SUT), sorbitol transporter (SOT), tonoplastic monosaccharide transporter (TMT) and sugar transporter protein (STP), which are special transporter proteins located on the vacuole membrane (Hu et al., 2014; Sauer, 2007; Büttner, 2007). The SUT mainly mediates the transport of sucrose and maltose (Sauer, 2007), and the SOT mainly mediates the transport of sorbitol (Hu et al., 2014). The TMT and STP mainly mediate the transmembrane transport of glucose, fructose and lactose (Büttner, 2007). Sucrose enters the cell as sucrose or as hexose and is first hydrolyzed into glucose and fructose by cell wall invertase (CWINV) (Persia et al., 2008), which is related to plant stress resistance (Albacete et al., 2015). In sink cells, the transported sugars are either metabolized or stored. In the cytoplasm, there are a variety of enzymes involved in sugar metabolism that form a complex regulatory network, including neutral invertase (NINV), sucrose phosphate synthase (SPS) (Hashida et al., 2016; Yativ et al., 2010) and sucrose synthase (SUS) (Klotz and Haagenson, 2008). Vacuolar acid invertase (VAINV) can convert sucrose to fructose and glucose (Lin et al., 2015) after sucrose is transported into the vacuole (Chen et al., 2017). Sorbitol is synthesized in source tissues, such as chloroplast cells, by sorbitol-6-phosphate dehydrogenase (S6PDH) (Kim et al., 2015). In chloroplast cells, sorbitol is also hydrolyzed into hexose by sorbitol dehydrogenase (SDH). 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 $kJ \cdot m^{-2} \cdot d^{-1}$ 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 $kJ \cdot m^{-2} \cdot d^{-1}$ 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 $kJ \cdot m^{-2} \cdot d^{-1}$, 1.44 $kJ \cdot m^{-2} \cdot d^{-1}$ and 2.16 $kJ \cdot m^{-2} \cdot d^{-1}$ from
127 February 2015 to May 2015. The control supplemental UV-B dose was 0 $kJ \cdot m^{-2} \cdot d^{-1}$.
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 $kJ \cdot m^{-2} \cdot d^{-1}$ from February 2016 to May 2016 and supplemental
136 UV-B radiation dose was 1.44 $kJ \cdot m^{-2} \cdot d^{-1}$ with supplemental 0 $kJ \cdot m^{-2} \cdot d^{-1}$ UV-B dose
137 as control, and all other conditions being the same with screening for the optimum
138 UV-B radiation dose.

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

Fresh and dry weight measurements

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

Total anthocyanin extraction and measurement

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

D_λ = (A530-A620) - 0.1(A650-A620) and

Anthocyanins content (mμg·g^{-1}) = $\frac{OD\lambda}{\xi\lambda} \times \frac{V}{W} \times 106$,

where ξλ (Anthocyanin molecule's 530 nm light extinction coefficient) = 4.62 × 104, V indicates the total volume of the extract; W indicates the sample weight (g FW: Fresh weight); and 106 is the number of molecules of mg in mμg.

Chlorophyll and carotenoid extractions and measurements

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

chlorophyll and carotenoid contents were calculated using the following equations:

Ca = 13.95 D665 - 6.88 D649;

Cb = 24.96 D649 - 7.32 D665;

$$Cx{\cdot}c = \frac{1000\,D470 - 2.05\,Ca - 114.8\,Cb}{245};\ \text{and}$$

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

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

Total phenolics and phenolic components extractions and measurements

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

High-performance liquid chromatography (HPLC) was used for the identification and quantification of mature phenolic components of peach sarcocarp and pericarp in 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 NH_2 (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 μL 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 $NH_4H_2PO_4$ (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×250 mm) column. Operating conditions were as
213 follows: column temperature was 28°C, injection volume was 10 μL, 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 sames 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.
240 Doe. gov/pz/portal. html). Primer 3 (http: //bioinfo. Ut. ee/primer3-0. 4.0/) was used
241 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 RNAprep 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

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

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

Statistical analyses

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

Results

1.44 kJ·m^{-2}·d^{-1} UV-B radiation increased the sugar content and decreased the

acid content

1.44 kJ·m^{-2}·d^{-1} UV-B radiation was the most effective in increasing the sugar content and reducing the acid content of the peach variety 'Tainongtiamnmi' in the three UV-B radiation intensities used in this study (Fig. 2). Its total sugar content was 1.5 times as much as that of the control.

Quality and appearance of 'Lumi 1' during the UV-B treatment

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

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

Under UV-B radiation total phenolics content in the flesh was mainly increased (Fig. S4A). In the pericarp total phenolics content did not significantly change compared with in the control (Fig. S4B). At the mature stage, only the protocatechuic 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

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

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

SUS and NINV enzyme activities and their gene expression levels were mainly increased of leaves during the UV-B treatment, while SPS, CWINV and VAINV enzymes and their gene expression levels did not change significantly (Fig. S8). SUT protein level first increased and then decreased, which was contrary to the accumulation of sugar in the flesh (Fig. S9A). STP and TMT protein and gene 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 CO_2 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 $kJ \cdot m^{-2} \cdot d^{-1}$ 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.,

436 2006). During UV-B treatment, the decreases in SUT, STP and TMT inhibited the
437 sucrose transport from leaves and pericarp to the fruit after after the slow-growth
438 period after the slow-growth period. Therefor, the fruit sugar content increased before
439 the second fruit-expansion stage due to the increased synthesis and transport of
440 sucrose in pericarp and inhibition of sucrose decomposition and transport in sarcocarp.
441 It had little correlation with the synthesis and translocation of sugars in leaf before
442 second fruit-expansion stage of peach fruit development. Sugars were decreased in
443 fruit after the slow-growth period, cause by the inhibition of sucrose decomposition
444 and transport in pericarp and leaf. This may have been caused by sink-source
445 relationships in fruit trees, in which, at the early stages of fruit development, the
446 competition for nutrients is greater than in mature fruits (Lenz, 1979).
447
448 *UV-B, sorbitol metabolism and translocation*
449 Sorbitol is mainly accumulated in source leaves in peach, and it constitutes up to
450 80% of the total solutes involved in osmotic adjustment (Bianco et al, 2000). Sorbitol
451 is found mainly in leaves. In Rosaceae fruit trees, such as apple, pear and peach, leaf
452 disc experiments showed enhanced sorbitol accumulation under salt, osmotic and
453 low-temperature stresses, and ABA-mediated S6PDH plays a role in sorbitol
454 biosynthesis in various stress responses (Kanayama et al., 2007). SDH exhibits the
455 highest activity on oxidized sorbitol (Aquayo et al., 2013; Jia et al., 2015). Yeast
456 transformed with the *MdSOTs* of apple had a significant sorbitol up-take (Watari et al.,
457 2004). During UV-B treatment, the changes in the sorbitol content were opposite to
458 those in the SDH activity in sarcocarp, peel and leaf. The SDH activity increased

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

464 *UV-B and plant stress resistance*

465 Under salt stress, *TMT2* was observed to increase in abundance (Pertlobermeyer
466 et al., 2016). Oxalic acid can significantly enhance the SUS cleavage function and
467 SOX activity, while it also increases the sugar (glucose and fructose) content (Wang et
468 al., 2016). Sucrose and sorbitol content were increased due to the *PpTMT* expression
469 levels and SUS and SOX activities increased in some periods of fruit development
470 after UV-B treatment in this experiment. Therefore, we speculate that UV-B treatment
471 may improve the resistance of peach trees but this requires further experimental
472 verification. Greenhouse experiments have numerous limiting factors, but in the
473 future studies under UV-B conditions, we will add other external factors, such as CO_2
474 or nitrogen, phosphorus and potassium, to further improve the fruit quality of peaches
475 grown in greenhouses. Related transcription factors that promote *PpSPS*, *PpSUS*,
476 *PpSUT* and *PpSOT* genes expression during UVB treatment of peach need to be
477 determined (Fig. 14). We hypothesize that the application in agricultural production
478 under greenhouse conditions of 1.44 $kJ \cdot m^{-2} \cdot d^{-1}$ UV-B radiation to peach before the
479 second fruit-expansion period can increase the soluble sugar content but not the
480 organic acids content.

481

Supplementary data

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

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

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

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

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

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

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

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

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

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

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

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

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

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

511 Acknowledgements

512 We thank Qingjie Wang for the technical assistance provided for this study. This work

513 was supported by the National Natural Science Foundation of China (3167213) and

514 the Natural Science Foundation of Shandong Province (ZR2014CM015).

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

520 References

521 **Aguayo MF, Ampuero D, Mandujano P, Parada R, Muñoz R, Gallart M,**

522 **Altabella T, Cabrera R, Stange C, Handford M.** 2013. Sorbitol dehydrogenase

523 is a cytosolic protein required for sorbitol metabolism in Arabidopsis thaliana.

524 Plant Science An International Journal of Experimental Plant Biology **205-206,**

525 63-75.

526 **Bianco RL, Rieger M, Sung SJS.** 2000 Effect of drought on sorbitol and sucrose

527 metabolism in sinks and sources of peach. Physiologia Plantarum **108,** 71–78.

528 **Büttner M.** 2007. The monosaccharide transporter(-like) gene family in Arabidopsis.
529 Febs Letters **581,** 2318–2324.

530 **Dekkers BJ, Schuurmans JA, Smeekens SC.** 2004. Glucose delays seed
531 germination in Arabidopsis thaliana. Planta **218,** 579-588.

532 **Campbell CD, Sage RF, Kocacinar F, Way DA.** 2005. Estimation of the whole-plant
533 CO2 compensation point of tobacco (Nicotiana tabacum L.). Global Change
534 Biology **11,** 1956-1967.

535 **Chen C, Yuan Y, Zhang C, Li H, Ma F, Li M.** 2017. Sucrose phloem unloading
536 follows an apoplastic pathway with high sucrose synthase in Actinidia fruit. Plant
537 Science **255,** 40-50.

538 **Crisosto C.** 2002. How do we increase peach consumption? Acta Horticulturae, **592,**
539 601-605.

540 **Desnoues E, Baldazzi V, Génard M, Mauroux JB, Lambert P, Confolent C,**
541 **Quilotturion B.** 2016. Dynamic QTLs for sugars and enzyme activities provide
542 an overview of genetic control of sugar metabolism during peach fruit
543 development. Journal of Experimental Botany **67,** 3419-3431.

544 **Elsa D, Yves G, Valentina B, Véronique S, Michel G, Bénédicte QT.** 2014. Profiling
545 sugar metabolism during fruit development in a peach progeny with different
546 fructose-to-glucose ratios. BMC Plant Biology **14,** 1-13.

547 **Eom JS, Cho JI, Reinders A, Lee SW, Yoo Y, Tuan PQ, Choi SB, Bang G, Park YI,**
548 **Cho MH.** 2011. Impaired Function of the Tonoplast-Localized Sucrose
549 Transporter in Rice, OsSUT2, Limits the Transport of Vacuolar Reserve Sucrose
550 and Affects Plant Growth. Plant Physiology **157,** 109-119.

Feng H, An L, Chen T, Qiang W, Xu S, Zhang M, Wang X, Cheng G. 2003. The effect of enhanced ultraviolet-B radiation on growth, photosynthesis and stable carbon isotope composition (δ 13 C) of two soybean cultivars (Glycine max) under field conditions. Environmental & Experimental Botany **49,** 1-8.

Fotopoulos V, Gilbert MJ, Pittman JK, Marvier AC, Buchanan AJ, Sauer N, Hall JL, Williams LE. 2003. The Monosaccharide Transporter Gene, , and the Cell-Wall Invertase, β, Are Induced in Arabidopsis during Infection with the Fungal Biotroph. Canadian Journal of Hospital Pharmacy **67,** 366-372.

Filip M, Vlassa M, Coman V, Halmagyi A. 2016. Simultaneous determination of glucose, fructose, sucrose and sorbitol in the leaf and fruit peel of different apple cultivars by the HPLC–RI optimized method. Food Chemistry 199: 653-659.

Gao Z, Maurousset L, Lemoine R, Yoo SD, Van NS, Loescher W. 2003. Cloning, expression, and characterization of sorbitol transporters from developing sour cherry fruit and leaf sink tissues. Plant Physiology **131,** 1566-1575.

Graeber K, Linkies A, Wood AT, Leubnermetzger G. 2011. A guideline to family-wide comparative state-of-the-art quantitative RT-PCR analysis exemplified with a Brassicaceae cross-species seed germination case study. Plant Cell **23,** 2045-2063

Hashida Y, Hirose T, Okamura M, Hibara KI, Ohsugi R, Aoki N. 2016. A reduction of sucrose phosphate synthase (SPS) activity affects sucrose/starch ratio in leaves but does not inhibit normal plant growth in rice. Plant Science **253,** 40-49.

Hu PZ, Ju YW, Gai HQ, Gai FY, Kai JQ, Li FW, Shao LZ. 2014. The role of

574 sucrose-metabolizing enzymes in pear fruit that differ in sucrose accumulation.
575 Acta Physiologiae Plantarum **36,** 71-77.

576 **Jia Y, Wong DC, Sweetman C, Bruning JB, Ford CM.** 2015. New insights into the
577 evolutionary history of plant sorbitol dehydrogenase. BMC Plant Biology **15,**
578 101.

579 **Kakani VG, Reddy KR, Zhao D, Sailaja K.** 2003. Field crop responses to
580 ultraviolet-B radiation: a review. Agricultural & Forest Meteorology **120,**
581 191-218.

582 **Kanayama Y, Moriguchi R, Deguchi M, Kanahama K, Yamaki S.** 2007. Effects of
583 environmental stresses and abscisic acid on sorbitol-6-phosphate dehydrogenase
584 expression in rosaceae fruit trees. Acta Horticulturae **738,** 375-381.

585 **Kato-Noguchi H, Yasuda Y, Sasaki R.** 2010. Soluble sugar availability of
586 aerobically germinated barley, oat and rice coleoptiles in anoxia. Journal of Plant
587 Physiology **167,** 1571-1576.

588 **Klann EM, Hall B, Bennett AB.** 1996. Antisense acid invertase (TIV1) gene alters
589 soluble sugar composition and size in transgenic tomato fruit. Plant Physiology
590 **112,** 1321-1330.

591 **Klotz KL, Haagenson DM.** 2008. Wounding, anoxia and cold induce sugarbeet
592 sucrose synthase transcriptional changes that are unrelated to protein expression
593 and activity. Journal of Plant Physiology **165,** 423-434.

594 **Kroger M, Meister K, Kava R.** 2006. Low□calorie Sweeteners and Other Sugar
595 Substitutes: A Review of the Safety Issues. Comprehensive Reviews in Food
596 Science & Food Safety **5,** 35-47.

Leskow CC, Kamenetzky L, Dominguez PG, Díaz Zirpolo JA, Obata T, Costa H, Martí M, Taboga O, Keurentjes J, Sulpice R. 2016. Allelic differences in a vacuolar invertase affect Arabidopsis growth at early plant development. Journal of Experimental Botany **67,** 4091.

Lin Y, Liu T, Liu J, Liu X, Ou Y, Zhang H, Li M, Sonnewald U, Song B, Xie C. 2015. Subtle regulation of potato acid invertase activity by a protein complex of StvacINV1-StInvInh2B-SbSnRK1. Plant Physiology.

Liu H, Cao J, Jiang W. 2015. Changes in phenolics and antioxidant property of peach fruit during ripening and responses to 1-methylcyclopropene. Postharvest Biology & Technology **108,** 111-118.

Liu L, Ji ML, Chen M, Sun MY, Fu XL, Li L, Gao DS, Zhu CY. 2016. The flavor and nutritional characteristic of four strawberry varieties cultured in soilless system. Food Science & Nutrition **4,** 858-868..

Loreti E, Bellis LD, Alpi A, Perata P. 2001. Why and How Do Plant Cells Sense Sugars? Annals of Botany **88,** 803-812.

Martínez-Lüscher J, Sánchezdíaz M, Delrot S, Aguirreolea J, Pascual I, Gomès E. 2014. Ultraviolet-B Radiation and Water Deficit Interact to Alter Flavonol and Anthocyanin Profiles in Grapevine Berries through Transcriptomic Regulation. Plant & Cell Physiology **55,** 1925-1936.

Martínez-Lüscher J, Sánchezdíaz M, Delrot S, Aguirreolea J, Pascual I, Gomès E. 2016. Ultraviolet-B alleviates the uncoupling effect of elevated CO2 and increased temperature on grape berry (Vitis vinifera cv. Tempranillo) anthocyanin and sugar accumulation. Australian Journal of Grape & Wine

620 Research **22,** 87-95.

621 **Nosarzewski M, Archbold DD.** 2007. Tissue-specific expression of SORBITOL
622 DEHYDROGENASE in apple fruit during early development. Journal of
623 Experimental Botany **58,** 1863-1872

624 **Oura Y, Yamada K, Shiratake K, Yamaki S.** 2000. Purification and characterization
625 of a NAD+-dependent sorbitol dehydrogenase from Japanese pear fruit.
626 Phytochemistry **54,** 567-572.

627 **Persia D, Cai G, Casino CD, Faleri C, Willemse MTM, Cresti M.** 2008. Sucrose
628 Synthase Is Associated with the Cell Wall of Tobacco Pollen Tubes. Plant
629 Physiology **147,** 1603-1618.

630 **Pertl-Obermeyer H, Trentmann O, Duscha K, Neuhaus HE, Schulze WX.** 2016.
631 Quantitation of Vacuolar Sugar Transporter Abundance Changes Using
632 QconCAT Synthtetic Peptides. Frontiers in Plant Science **7,** 411.

633 **Rolland F, Baena-Gonzalez E, Sheen J.** 2006. Sugar sensing and signaling in plants:
634 conserved and novel mechanisms. Annual Review of Plant Biology **57,** 675-709.

635 **Rottmann T, Zierer W, Subert C, Sauer N, Stadler R.** 2016. STP10 encodes a
636 high-affinity monosaccharide transporter and is induced under low-glucose
637 conditions in pollen tubes of Arabidopsis. Journal of Experimental Botany **67,**
638 2387-2399.

639 **Suzuki Y, Dandekar AM.** 2014. Sucrose induces expression of the
640 sorbitol-6-phosphate dehydrogenase gene in source leaves of loquat. Physiologia
641 Plantarum **150,** 355–362.

642 **Santiago-Doménech N, Jiménez-Bemúdez S, Matas AJ, Rose JKC,**

643 **Muñoz-Blanco J, Mercado JA, Quesada MA.** 2008. Antisense inhibition of a
644 pectate lyase gene supports a role for pectin depolymerization in strawberry fruit
645 softening. Journal of Experimental Botany **59,** 2769-2779.

646 **Sauer N.** 2007. Molecular physiology of higher plant sucrose transporters. Febs
647 Letters **581,** 2309-2317.

648 **Scattino C, Castagna A, Neugart S, Chan HM, Schreiner M, Crisosto CH,**
649 **Tonutti P, Ranieri A.** 2014. Post-harvest UV-B irradiation induces changes of
650 phenol contents and corresponding biosynthetic gene expression in peaches and
651 nectarines. Food Chemistry **163,** 51-60.

652 **Schumaker MA, Bassman JH, Robberecht R, Radamaker GK** (1997) Growth,
653 leaf anatomy, and physiology of Populus clones in response to solar ultraviolet-B
654 radiation. Tree Physiology **17,** 617-626.

655 **Singh S, Agrawal SB, Agrawal M.** 2015. Responses of pea plants to elevated UV-B
656 radiation at varying nutrient levels: N-metabolism, carbohydrate pool, total
657 phenolics and yield. Functional Plant Biology **42,** 1045-1056.

658 **Singleton VL, Rossi JA.** 1964. Colorimetry of Total Phenolics with
659 Phosphomolybdic-Phosphotungstic Acid Reagents. American Journal of Enology
660 & Viticulture **16,** 144–158.

661 **Teo G, Suzuki Y, Uratsu SL, Lampinen B, Ormonde N, Hu WK, Dejong TM,**
662 **Dandekar AM.** 2006. Silencing leaf sorbitol synthesis alters long-distance
663 partitioning and apple fruit quality. Proceedings of the National Academy of
664 Sciences of the United States of America **103,** 18842-18847.

665 **Tong Z, Gao Z, Fei W, Zhou J, Zhen Z.** 2009. Selection of reliable reference genes

for gene expression studies in peach using real-time PCR. BMC Molecular Biology **10,** 1-13.

Trentin AR, Pivato M, Mehdi SM, Barnabas LE, Giaretta S, Fabregaprats M, Prasad D, Arrigoni G, Masi A. 2015. Proteome readjustments in the apoplastic space of Arabidopsis thaliana ggt1 mutant leaves exposed to UV-B radiation. Frontiers in Plant Science **1,** 128.

Vanhaelewyn L, Schumacher P, Poelman D, Fankhauser C, Straeten DVD, Vandenbussche F. 2016. Reference of ultraviolet-b photomorphogenesis function allows efficient phototropin mediated ultraviolet-B phototropism in etiolated seedlings. Plant Science An International Journal of Experimental Plant Biology **252,** 215-221.

Verde I, Abbott AG, Scalabrin S, Jung S, Shu S, Marroni F, Zhebentyayeva T, Dettori MT, Grimwood J. 2013. The high-quality draft genome of peach (Prunus persica) identifies unique patterns of genetic diversity, domestication and genome evolution. Nature Genetics **45,** 487-494.

Vimolmangkang S, Zheng H, Peng Q, Jiang Q, Wang H, Fang T, Liao L, Wang L, He H, Han Y. 2016. Assessment of Sugar Components and Genes Involved in the Regulation of Sucrose Accumulation in Peach Fruit. Journal of Agricultural & Food Chemistry **64,** 6723-6729.

Vizzotto G, Pinton R, Varanini Z, Costa G. 1996. Sucrose accumulation in developing peach fruit. Physiologia Plantarum **96,** 225-230.

Wang D, Gao Z, Du P, Xiao W, Tan Q, Chen X, Li L, Gao D. 2015. Expression of ABA Metabolism-Related Genes Suggests Similarities and Differences Between

689 Seed Dormancy and Bud Dormancy of Peach (Prunus persica). Frontiers in Plant
690 Science **6,** 1248.

691 **Wang Z, Cao J, Jiang W.** 2016. Changes in sugar metabolism caused by exogenous
692 oxalic acid related to chilling tolerance of apricot fruit. Postharvest Biology &
693 Technology **114,** 10-16.

694 **Watari J, Kobae Y, Yamaki S, Yamada K, Toyofuku K, Tabuchi T, Shiratake K.**
695 2004. Identification of sorbitol transporters expressed in the phloem of apple
696 source leaves. Plant & Cell Physiology **45,** 1032-1041.

697 **Wijewardana C, Henry WB, Gao W, Reddy KR.** 2016. Interactive effects on CO_2,
698 drought, and ultraviolet-B radiation on maize growth and development. Journal
699 of Photochemistry & Photobiology B Biology **160,** 198-209.

700 **Wormit A, Trentmann O, Feifer I, Lohr C, Tjaden J, Meyer S, Schmidt U,**
701 **Martinoia E, Neuhaus HE.** 2006. Molecular identification and physiological
702 characterization of a novel monosaccharide transporter from Arabidopsis
703 involved in vacuolar sugar transport. Plant Cell **18,** 3476-3490.

704 **Wang XL, Xu YH, Peng CC, Fan RC, Gao XQ.** 2009. Ubiquitous distribution and
705 different subcellular localization of sorbitol dehydrogenase in fruit and leaf of
706 apple. Journal of Experimental Botany **60,** 1025-1034.

707 **Yamaguchi H, Kanayama Y, Yamaki S.** 1994. Purification and Properties of
708 NAD-Dependent Sorbitol Dehydrogenase from Apple Fruit. Plant & Cell
709 Physiology **35,** 887-892.

710 **Yamaki S.** 2007. Properties and functions of sorbitol-6-phosphate dehydrogenase,
711 sorbitol dehydrogenase and sorbitol oxidase in fruit and cotyledon of apple

(Malus pumila Mill. var. domestica Schneid.). Soviet Powder Metallurgy & Metal Ceramics **10,** 568-572.

Yamaki S. 2010. Metabolism and accumulation of sugars translocated to fruit and their regulation. Journal of the Japanese Society for Horticultural Science **79,** 1-15.

Yao YX, Dong QL, You CX, Zhai H, Hao YJ. 2011. Expression analysis and functional characterization of apple MdVHP1 gene reveals its involvement in Na(+), malate and soluble sugar accumulation. Plant Physiology & Biochemistry Ppb **49,** 1201-1208.

Yativ M, Harary I, Wolf S. 2010. Sucrose accumulation in watermelon fruits: Genetic variation and biochemical analysis. Journal of Plant Physiology **167,** 589-596

Yuan L, He LL, Zu YQ. 2010. Intraspecific variation in sensitivity to ultraviolet-B radiation in endogenous hormones and photosynthetic characteristics of 10 wheat cultivars grown under field conditions. South African Journal of Botany **76,** 493-498.

Zanon L, Falchi R, Hackel A, Kühn C, Vizzotto G. 2015. Expression of peach sucrose transporters in heterologous systems points out their different physiological role. Plant Science An International Journal of Experimental Plant Biology **238,** 262-272.

Zanon L, Falchi R, Santi S, Vizzotto G. 2015. Sucrose transport and phloem unloading in peach fruit: potential role of two transporters localized in different cell types. Physiologia Plantarum **154,** 179-193.

Zhang ZS, Jin LQ, Li YT, Tikkanen M, Li QM, Ai XZ, Gao HY. 2016. Ultraviolet-B Radiation (UV-B) Relieves Chilling-Light-Induced PSI Photoinhibition And Accelerates The Recovery Of CO_2 Assimilation In Cucumber (Cucumis sativus L.) Leaves. Scientific Reports **6,** 34455.

Zheng Y, Crawford GW, Chen X. 2014. Archaeological evidence for peach (Prunus persica) cultivation and domestication in China. Plos One **9,** e106595

Table and figures title

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

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

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

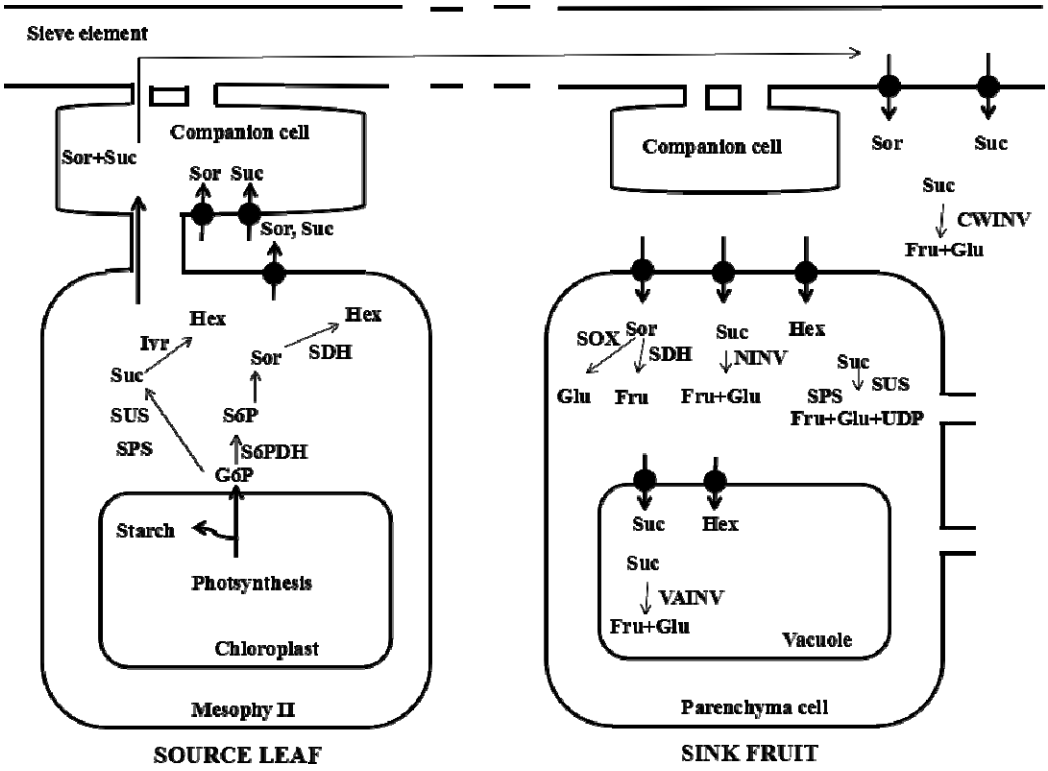
772 **Fig. 7.** Effects of UV-B treatment on SPS, SUS and SUT activity before the second
773 fruit-expansion stages in pericarp. (A) SPS activity and gene expression levels (*P <
774 0.05). (B) SUS activity and gene expression levels (*P < 0.05). (C) SUT activity and
775 gene expression levels (*P <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

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

822 **Fig. 1.**

823



824

825

826

827

828

829

830

831

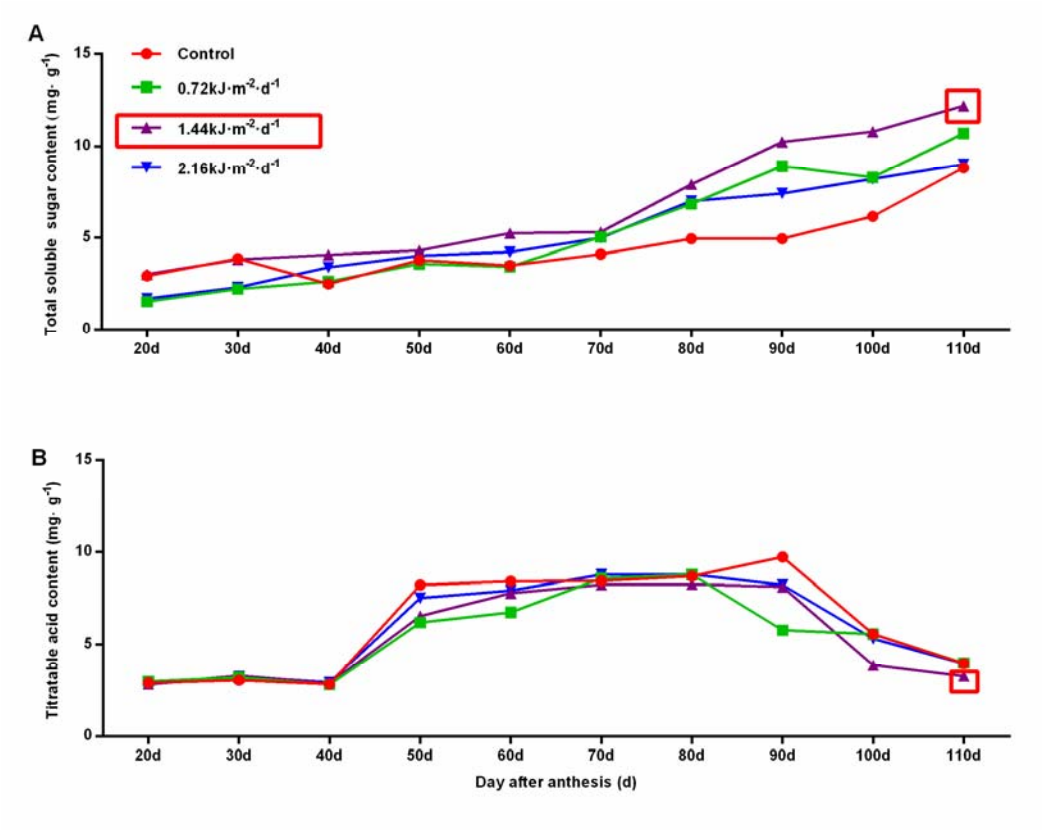
832

833

834

835 **Fig. 2.**

836



837

838

839

840

841

842

843

844

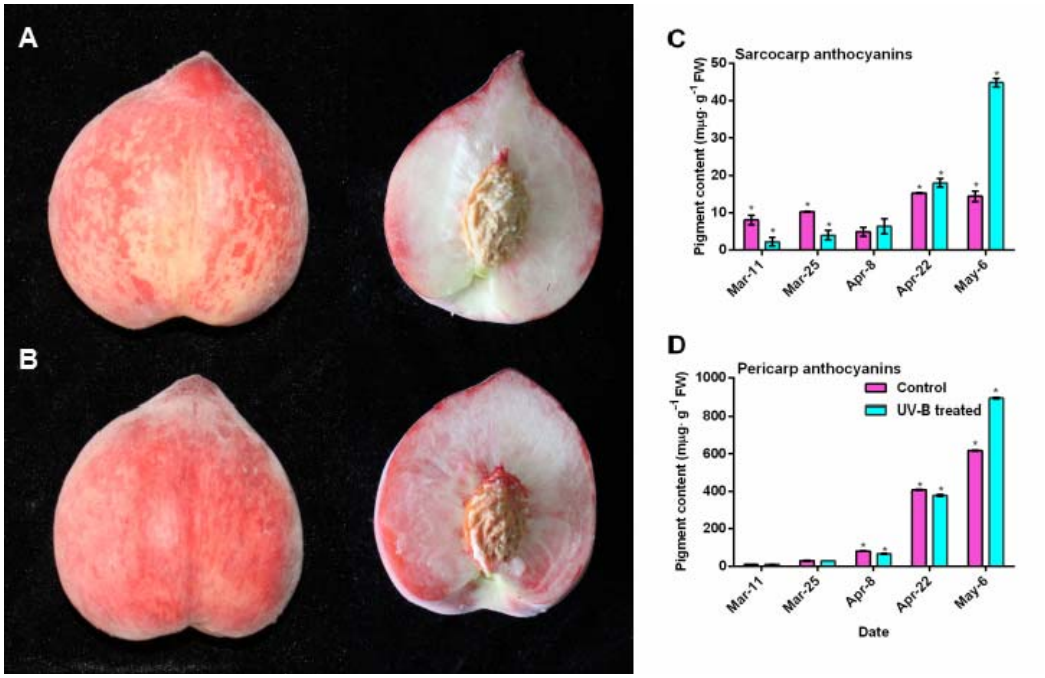
845

846

847

848 **Fig. 3.**

849



850

851

852

853

854

855

856

857

858

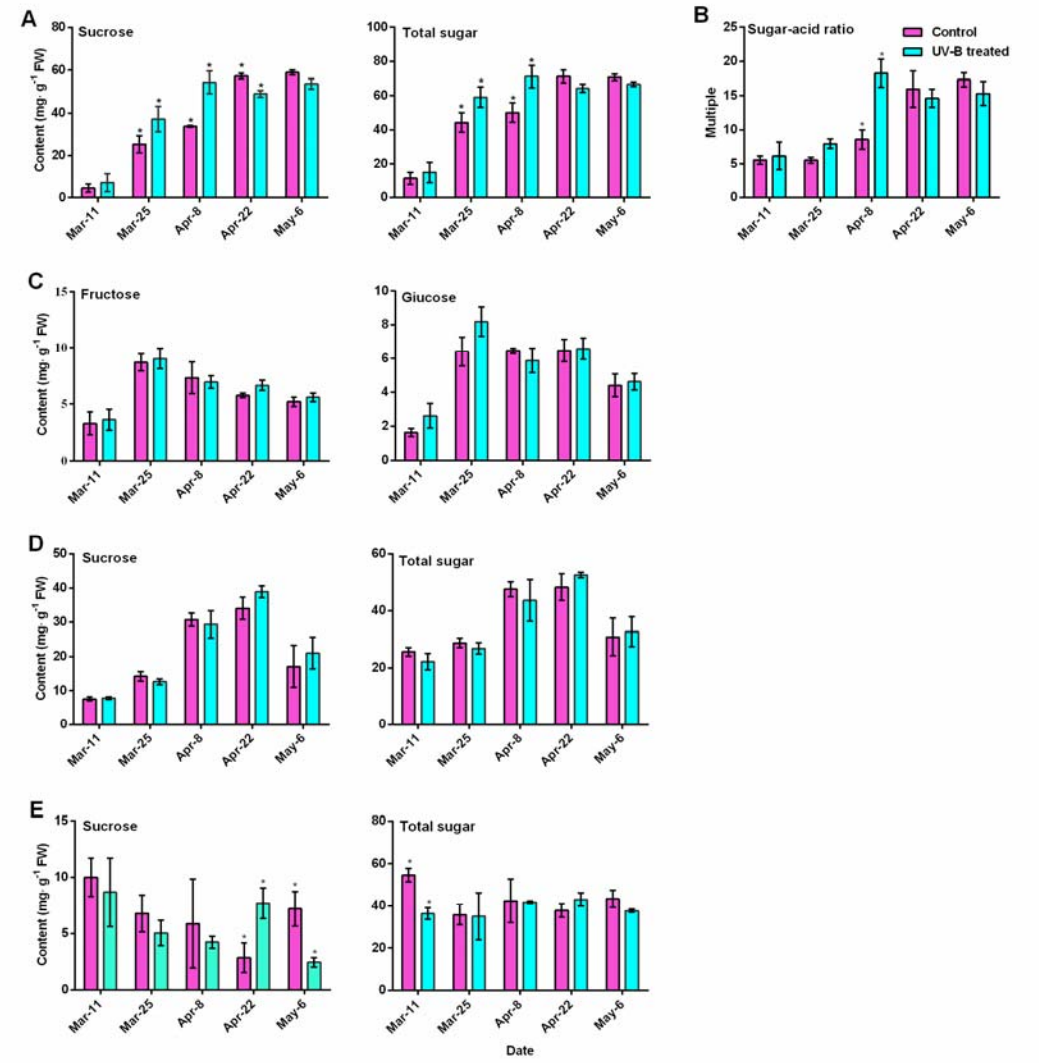
859

860

861

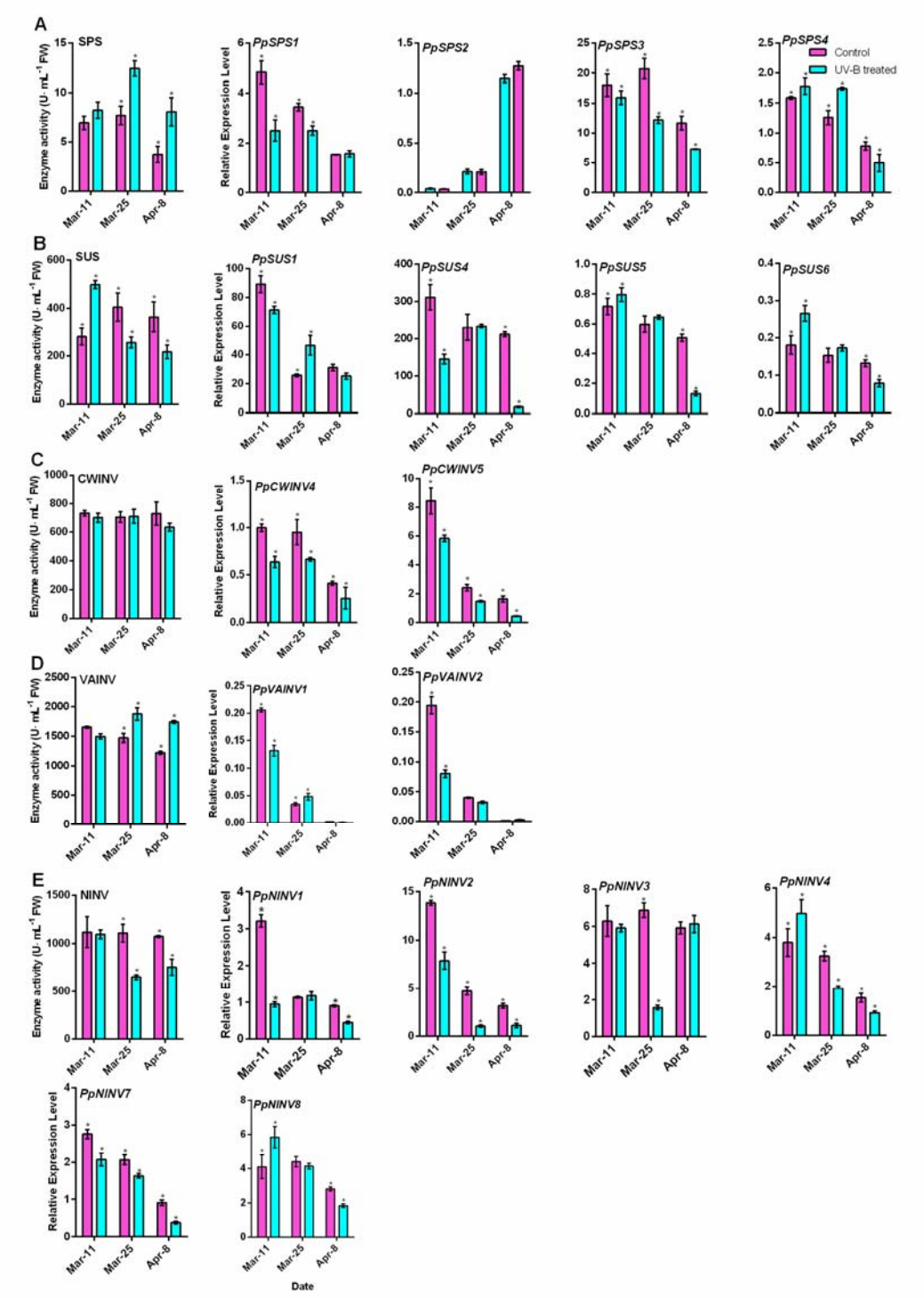
862

Fig. 4.



872 **Fig. 5.**

873

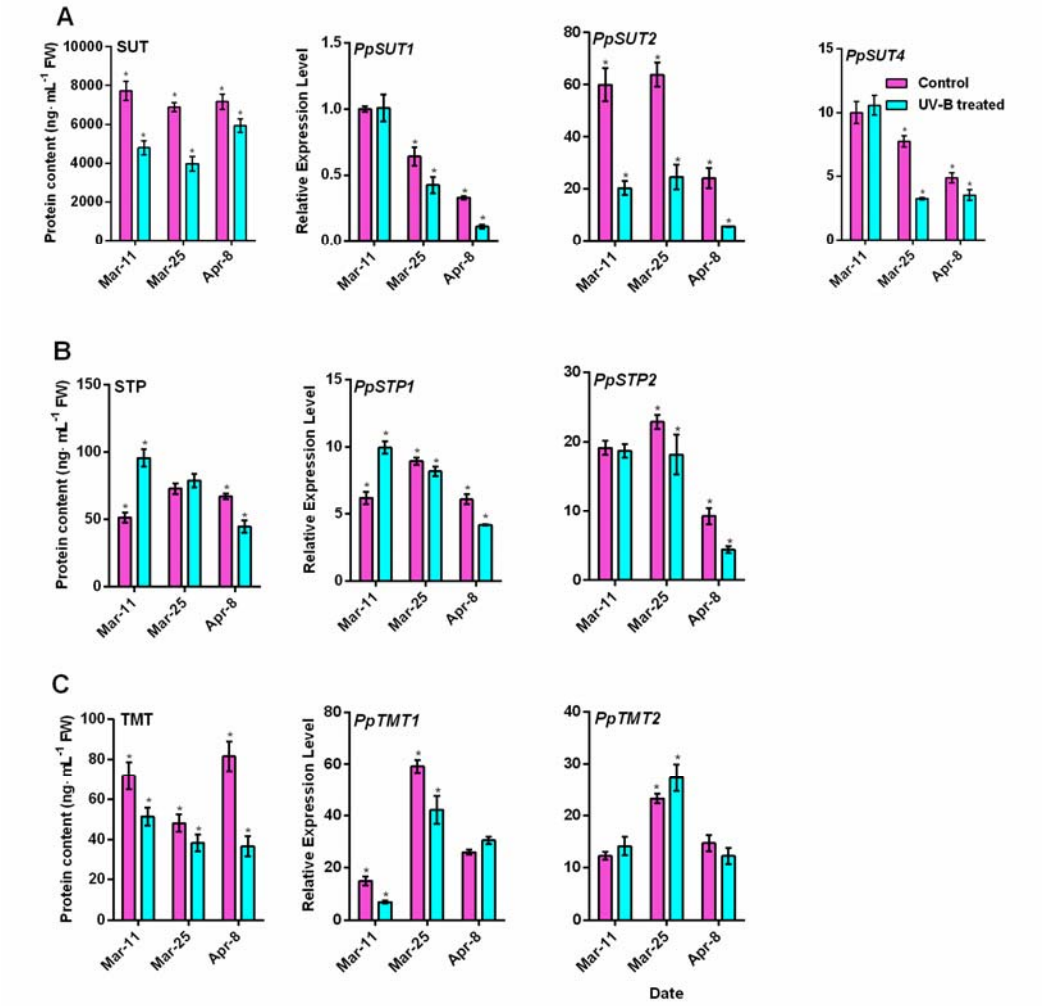


874

875

876 **Fig. 6.**

877



878

879

880

881

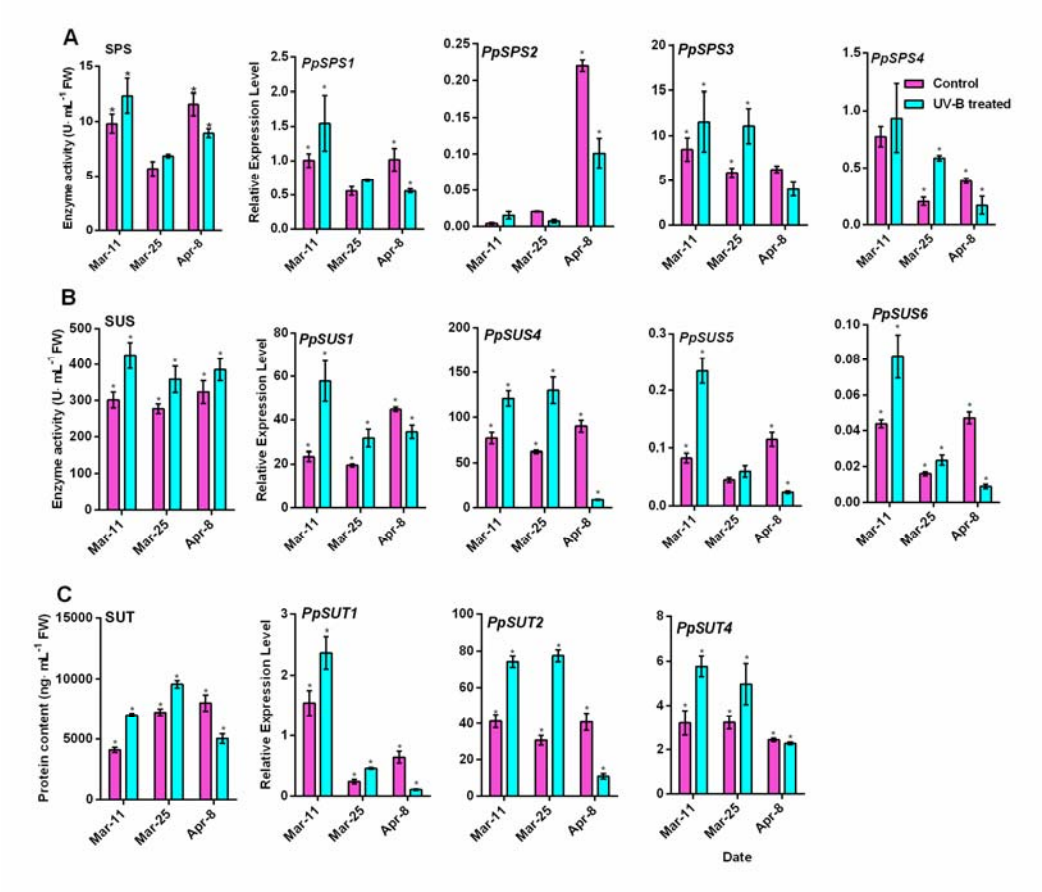
882

883

884

885 **Fig. 7.**

886



887

888

889

890

891

892

893

894

895

896

Fig. 8.

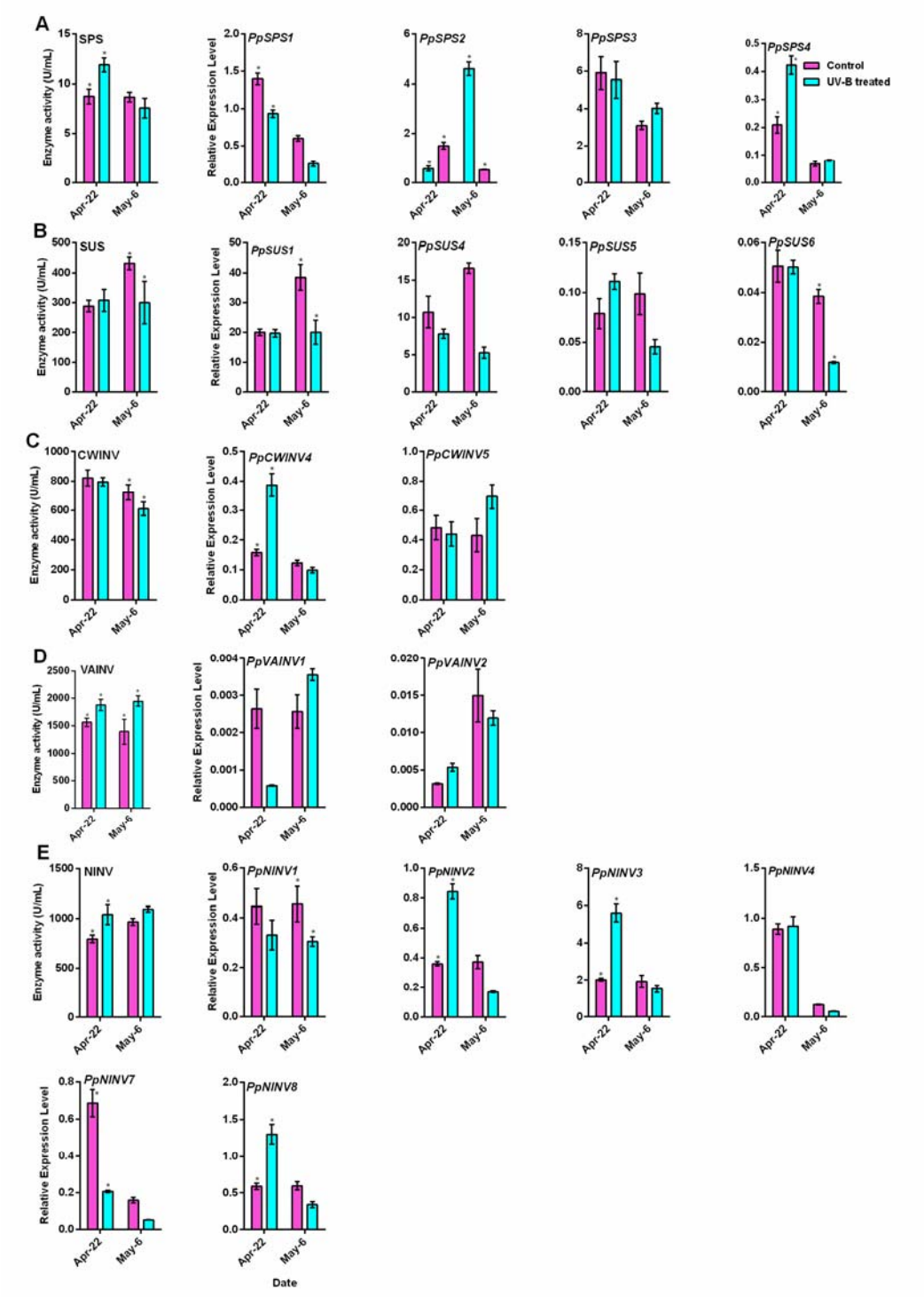


Fig. 9.

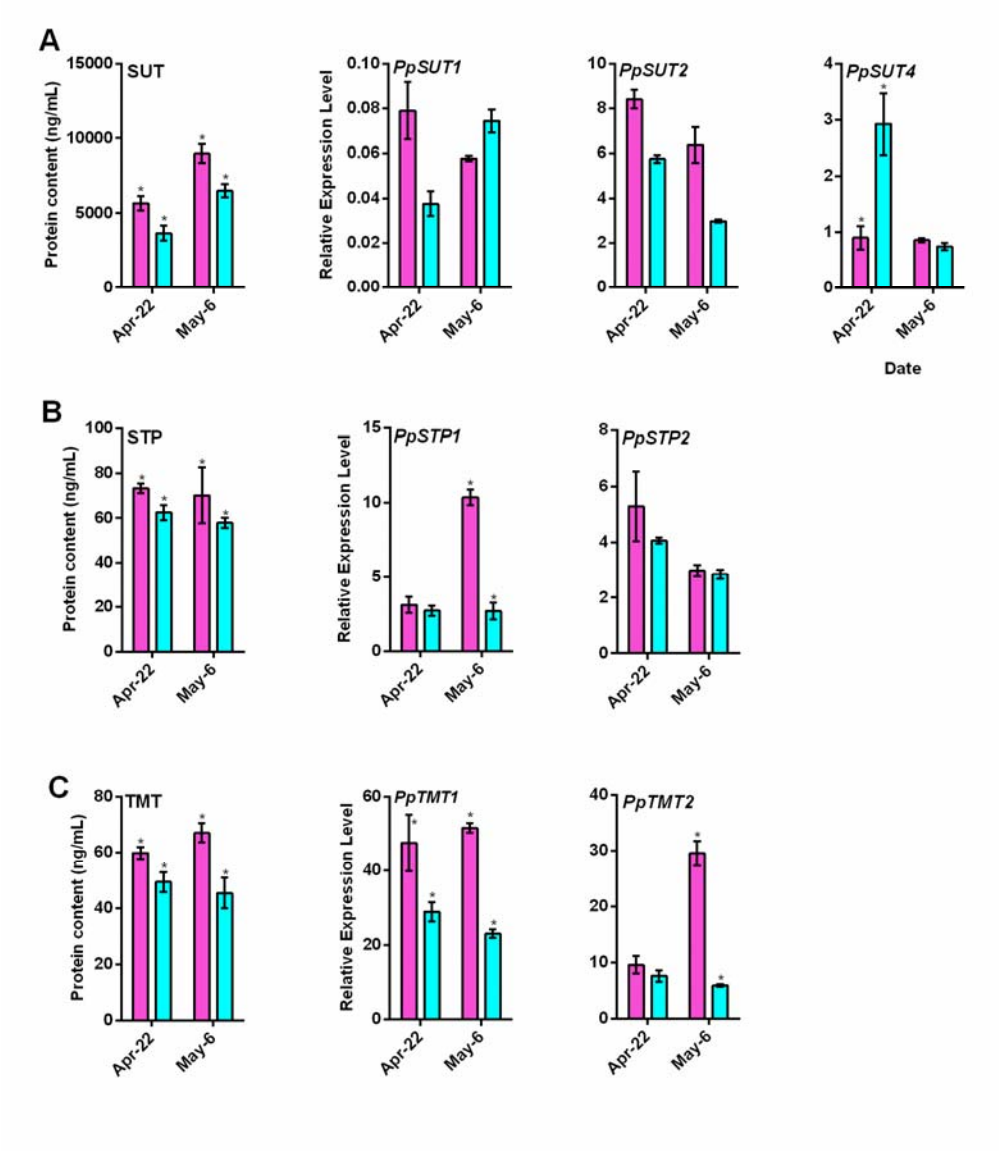


Fig. 10.

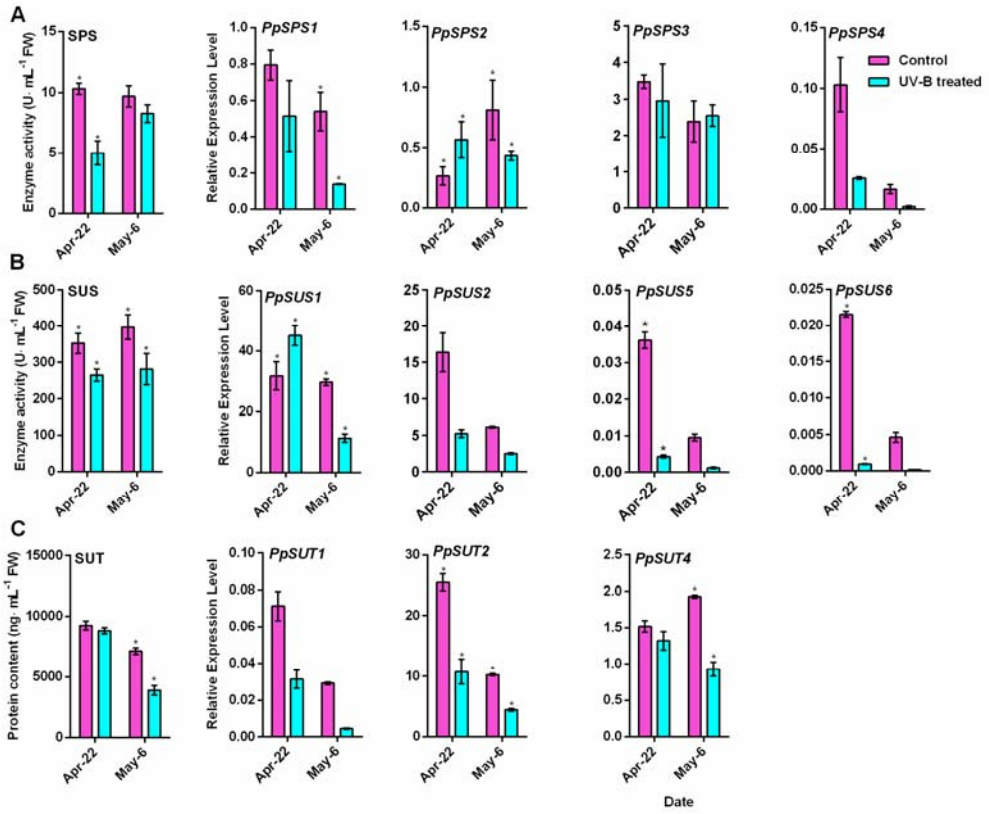
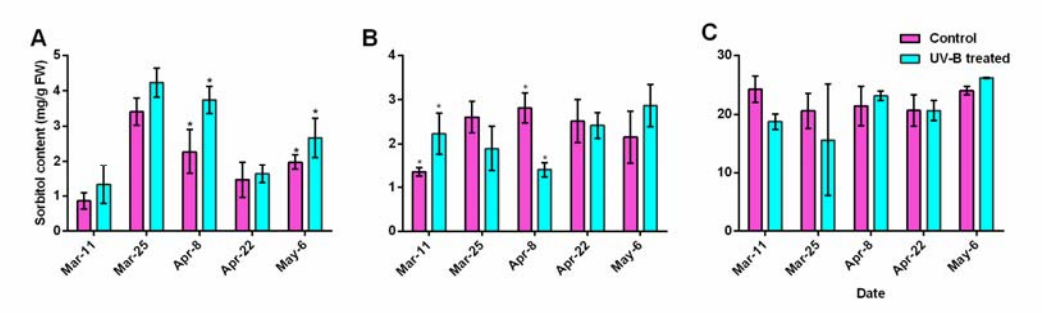
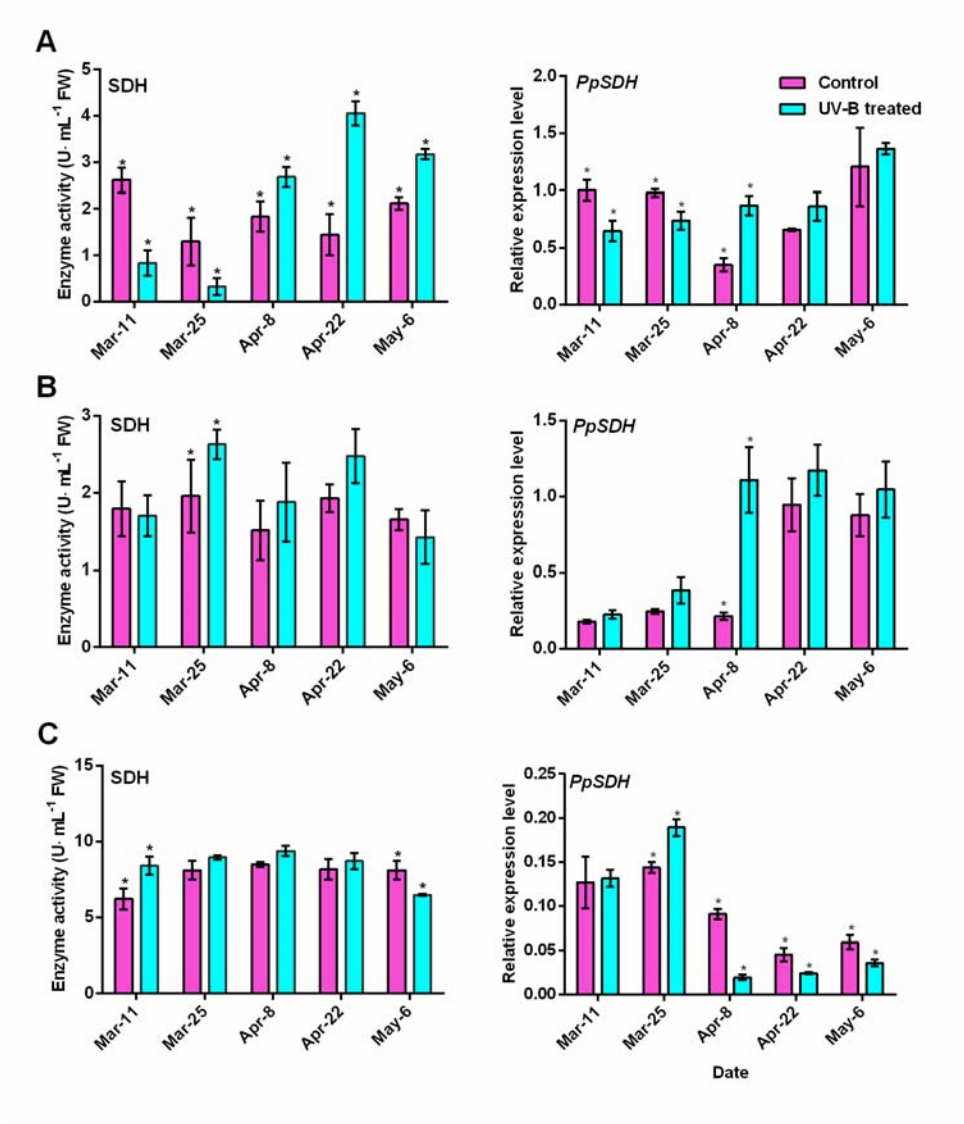


Fig. 11.



940 **Fig. 12.**

941



942

943

944

945

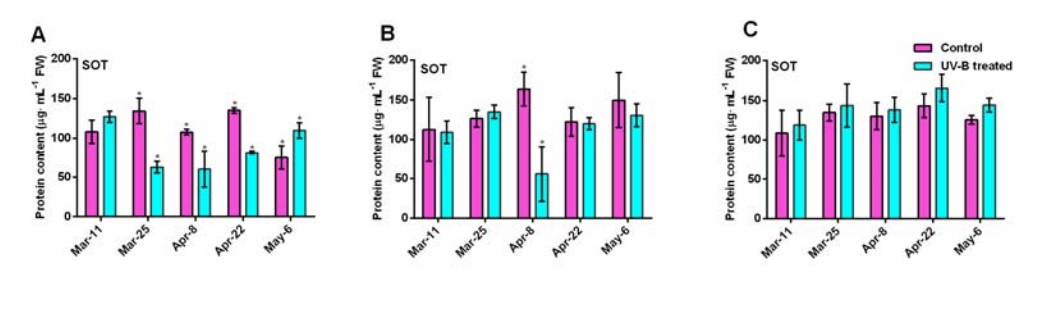
946

947

948

949 **Fig. 13.**

950



951

952

953

954

955

956

957

958

959

960

961

962

963

964

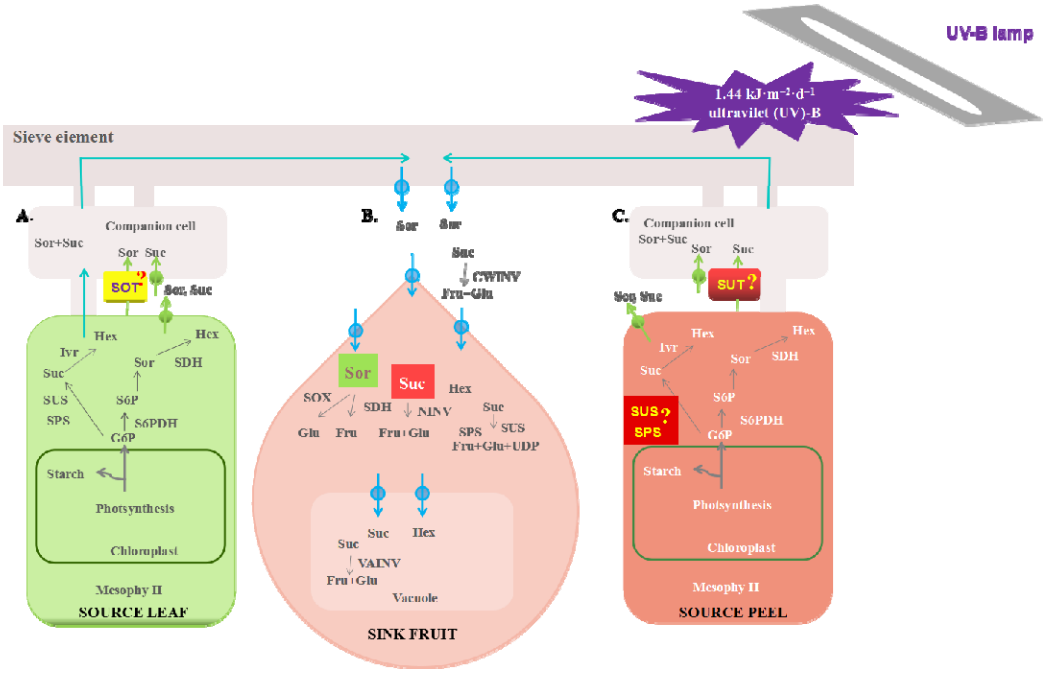
965

966

967

968 **Fig. 14.**

969



970