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Research article

Metabolic features underlying the response of sweet cherry fruit to postharvest UV-C irradiation

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ABSTRACT

The impact of ultraviolet-C (UV–C) irradiation on sweet cherry fruit was studied. Following harvest, fruits (cv. Sweetheart) were exposed to different doses of UV-C (0, 1.2, 3.0 or 6.0 kJ m^{-2}) and then cold stored (0 °C) for 10 days. Treatments with UV-C delayed most ripening features and reduced pitting symptoms, particularly following prolonged UV-C application. Also, application of the highest UV-C dose inhibited pectin degradation and delayed skin resistance to penetration. An activation of antioxidants capacity and bioactive compounds, such as flavonoids and phenolics was observed. Illumination with UV-C diminished respiration and altered metabolite profile in whole fruit and skin samples. Several amino acids (eg., threonine and aspartate), sugars, (eg., glucose and fructose) and alcohols (e.g., inositol and mannitol) were modulated by long-term UV-C treatment in whole cherry fruit. Various metabolites, including malate, galacturonate, oxoproline and glutamine were also modulated by UV-C skin tissue. These data enhance our understanding of UV-C function in fruit biology.

1. Introduction

Sweet cherry is one of the most popular temperate fruits which is highly appreciated by consumers worldwide (Karagiannis et al., 2018a). However, sweet cherries are extremely difficult to handle after harvest (shelf life of 7–14 days) since they are very susceptible to fruit softening and stem browning (Param and Zoffoli, 2016; Wade and Bain, 1980). In addition, sweet cherry is characterized by high transpiration rate, susceptibility to fungal rots and vulnerability to physiological disorders such as pitting, all of which limit its market life (Chockchaisawasdee et al., 2016). Therefore, the need to maintain cherry fruits for a long time is of great interest both for fruit marketing and for ensuring quality characteristics.

Although numerous technologies have been developed for extending sweet cherries shelf life, the need for environmentally-friendly technologies has turned the attention to solutions that focus on the alternation of fruit metabolism with minimal impact on their quality (Ziogas et al., 2018). Among the alternative methods for controlling postharvest fruit senescence, ultraviolet-C (UV–C) illumination appears to be one of the most attractive (Urban et al., 2016; Xu et al., 2017). Compared with UV-B (280–320 nm), UV-C (200–280 nm) due to its shorter wave is more effective for food products surface sterilization. Apart from that, it has been reported that short (for 3 and 5 min) exposure to UV-C irradiation can delay ripening and senescence in a variety of fruits such as apples (Lu et al., 1991), peaches (Gonzalez-Aguilar et al., 2004), persimmons (Imaizumi et al., 2018), strawberries (Li et al., 2014) and tomatoes (Bu et al., 2014; Pinheiro et al., 2015; Mditshwa et al., 2017). Also, it has been suggested that fruits pre-storage exposure to UV-C irradiation has as a consequence the activation of secondary metabolism (Liu et al., 2018; Pérez-Ambrocio et al., 2018; Sheng et al., 2018; Xu et al., 2019b).

The cherry skin is the physical barrier between fruit flesh tissue and environment, however stress factors like exposure to high energy by application of UV-C irradiation could alter cuticle composition and structure during postharvest period (Belge et al., 2014). As the outermost tissue of cherry, the cherry skin, plays an important role in protecting and preserving fruit storage life, and its metabolic features through intense respiration activity are closely related to fruit senescence (Sekse, 1993). Nevertheless, there is limited research regarding the impact of postharvest UV-C irradiation on the metabolism of cherry skin tissue. The aim of this study was, therefore, to explore the physiological and metabolic effects of time-dependent exposure to UV-C in both skin tissue and whole cherry fruit following cold storage.

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2. Materials and methods

2.1. Plant material and UV-C irradiation treatments

Sweet cherry (cv. Sweetheart) fruits were harvested from a commercial orchard in North Greece (Pella, Agia Fotini). To study the post-harvest UV-C irradiation effect, fruits were sampled at commercial harvest stage (ripening index: total soluble solids/acids ratio was 12) and then transferred to Pomology Laboratory of Aristotle University of Thessaloniki (Thessaloniki). Cherries were subjected to hydro-cooling (water temperature at 0 °C, for 10 min) and then were randomly divided into four subgroups (5 Kg fruit per subgroup). Afterwards, fruits were exposed to UV-C irradiation treatment for 0, 1.0, 2.5 or 5.0 min (on both sides for the half duration) in a modified fruit drying machine to which four UV-C lamps had been incorporated (OSRAM HNS 55W OFR G13, 26 mm diameter and 895 mm length). The distance between the lamps and the fruit was 50 cm and the intensity was 20 W m^{-2}. The UV dose was determined with a pyranometer (Kipp & Zonen CM5 pyranometer) connected on data logger (Delta-T Devices Ltd, DL3000). Thus, fruits were submitted to the four following treatments: Control (0 min UV-C), UV-C 1 min (1 min UV-C = 1.2 kJ m^{-2}), UV 2.5 min (2.5 min UV-C = 3 kJ m^{-2}), and UV 5 min (5 min UV-C = 6 kJ m^{-2}). All fruits were exposed to air flow for 10 min to remove free water on fruit surface and then were preserved in a cold storage room (0 °C, RH 95%) for 10 days. Following cold storage and after fruits temperature stabilization at 20 °C the post-harvest changes of fruit quality parameters were evaluated. Three replications of 10 fruits per treatment were sampled by cutting each fruit in two unequal pieces (3:4 and 1:4) and then frozen separately in liquid nitrogen. Cherry fruit skin tissue was separated from the rest frozen tissue of the ¾ fruit piece with a razor (a maximum of 1 mm corresponding to the epidermal cells were sampled) homogenized frozen and stored at −80 °C for further analysis. In this study the term 'skin' is referred to the aforementioned sampled tissue which contains a few cell layers from the epicarp and the mesocarp. All analyses were performed on both the whole fruit and the skin samples.

2.2. Fruit quality

2.2.1. Color parameters

Color indicator chroma (C^*), hue angle (h^0) and lightness (L^*) were recorded (McGuire, 1992). Chroma [C^* = (a*2 + b*2) 0.5] and hue angle [h° = arc tan (b*/a*)] were calculated from CIE a^*- and b^*-values, which a^* represent the gradation of color from green to red and b^* represent the gradation of color from yellow to blue and L^* the intensity from white to black (meter scale: 0-black to 100-white)were measured in thirty fruits per treatment. Color parameters L^*, a^*, b^* were recorded using a colorimeter (model Minolta CR-200 Minolta, Osaka, Japan) which was calibrated in white plate (Minas et al., 2016).

2.2.2. Textural properties of flesh tissue

Textural properties of thirty fruits per treatment, namely stem removal and penetration force were determined using Texture Analyzer TA XT2i (Stable Microsystems, Godalming, Surrey, UK) (Goulas et al., 2015). Fruit firmness was expressed as skin penetration force; the maximum force was recorded during penetration at 5 mm depth using a 6-mm diameter stainless steel cylindric probe. For stem removal, a tensile grip was used to remove the stem with traction force; the fruit was placed beneath a plate having a round hole (10 mm diameter) through which the stem was directed to the grip. To all measurements, the speed of arm was 0.8 mm s^{-1}. Results were expressed in Newtons (N).

2.2.3. Respiration rate and ripening index

Three batches of ten fruits were enclosed in 2-L air-tight jars for 30 min at 20 °C. Respiration rate was measured by evaluating fruits CO_2 production using a 1 mL gas sample drawn from the jars and injected into the gas chromatograph (Shimadzu GC-2014, Kyoto, Japan). Correction for CO_2 concentration was calculated by subtracting the ppm CO_2 of the laboratory CO_2 titer from that detected in the jars. The results were expressed as mL CO_2 kg^{-1} h^{-1}. Soluble solids concentration (SSC, ^{0} Brix) were determined in the juice from three replicates of ten fruits per treatment with a digital refractometer (Atago PR-101, Atago Co. Ltd., Japan) and TA, % malate. Titratable acidity was determined by potentiometric titration with 0.1 N NaOH up to pH 8.2, using 10 mL of diluted juice in 100 mL dH_2O. Fruit ripening index (RI) was calculated by the ratio of SSC to TA.

2.2.4. Evaluation of surface pitting

Subjective estimation of fruit physiological defects was performed for surface pitting at 10 days after cold storage, as follows. Surface pitting was divided in 6 classes: 0 (no pitting), 1 (pitting area < 0.1 cm^2), 2 (pitting area < 0.3 cm^2), 3 (pitting area < 0.6 cm^2), 4 (pitting area < 1 cm^2) and 5 (pitting area ≥1 cm^2). Evaluation was conducted in triplicate using 50 fruits per replicate. The results were expressed as % surface pitting for each treatment within each class.

2.3. Determination of total phenols, antioxidant capacity, total anthocyanins, tannins, flavonoids and hydroxycinnamic acids

The extraction of polyphenolic substances was conducted according to Asami et al. (2003). Total phenols and tannins were determined using Folin-Ciocalteu method (Asami et al., 2003). Optical density was measured at 760 nm in a microplate reader (Tecan infinite M200 PRO). Results were expressed in equivalents of mg Gallic acid 100 g^{-1} FW. For the calculation of tannins concentration, the polyphenolic extract was incubated with polyvinyl polypyrrolidone (PVPP) for tannins absorption (ratio extract: PVPP, 30:1, v/w) and optical density of the residual phenolic solution was subtracted from that of total phenols (Makkar et al., 1993); $A_{tannin} = A_{total\ phenols} - A_{residual\ phenols}$ (Supplementary Table S1). Antioxidant activity was determined using ferric reducing/antioxidant power (FRAP) (Benzie and Strain, 1996) and results were expressed in equivalents of mg Trolox 100 g^{-1} FW (Supplementary Table S1). Flavonoids was measured at 510 nm according to Cvek et al. (2007). Results were expressed as equivalents of mg rutin 100 g^{-1} FW, according to standard reference curve (Supplementary Table S1). Total anthocyanins and hydroxycinnamic acids were determined as reported by Obied et al. (2005). The results were respectively expressed in equivalents of mg cyanidin and caffeic acid 100 g^{-1} FW (Supplementary Table S1). All the above-mentioned data were analyzed in skin and whole fruit samples and were also expressed as ratio between skin and fruit transformed to log base two, positive values represent higher abundance in skin and negative values represent lower abundance in skin. Measurements were performed using three biological replicates.

2.4. Analysis of pectin fractions

Extraction of cell-wall material and determination of water-soluble and -insoluble pectin fractions was performed (Manganaris et al., 2007) to the skin tissue of thirty fruits per replication and treatments. Skin tissue (0.5g) was boiled in 95% pure ethanol for 20 min and homogenized in mechanical blender. Following centrifugation (10500 × g, 10 min) the supernatant was discarded. The pellet was washed with 80% acetone until clarified and then dried in oven at 60 °C constituting the cell-wall material (CWM). For obtaining the water-soluble pectin fraction 10 mg of CWM were dissolved in 4 mL dH_2O and after gentle shaking for 1 h and centrifugation (10500 × g, 10 min) the supernatant was collected. In the pellet 2 mL pure H_2SO_4 and 1 mL dH_2O were added and after centrifugated (8000 × g, 5 min), the supernatant was collected and constitutes the water-insoluble pectin fractions.

For pectin fractions 0.2 mL of water-soluble or 0.2 mL of water-

insoluble pectin fraction were mixed with 1.2 mL $Na_2B_4O_7$ (12.5 mM) in pure H_2SO_4, vortexed and placed in boiling water for 5 min. After that they were immediately transferred on ice and 20 μL m-hydroxybiphenyl (0.15%) in NaOH (0.5%) were added and the absorbance was measured at 520 nm (Tecan infinite M200 PRO). In parallel for each sample the same assay was conducted without the addition of 20 μL m-hydroxybiphenyl for internal correction. The results were expressed in equivalents of mg galacturonate g^{-1} CWM, based on standard curve of galacturonate (Supplementary Table S2).

2.5. Polar metabolite profiling

Determination of primary polar metabolites was performed in skin and whole fruit samples, as described by Lisec et al. (2006) with slight modifications. Extraction of frozen skin and fruit tissue (0.5 g) was as described by Michailidis et al. (2017). Briefly, 1400 μL methanol and 100 μL adonitol (0.2 mg mL^{-1}) was added with tissue and incubated for 10 min at 70 °C. Following centrifugation, the supernatant was reserved and 750 μL chloroform and 1500 μL dH_2O were added to the supernatant. An aliquot (150 μl) of the upper polar phase was dried, re-dissolved in 40 μL methoxyamine hydrochloride (20 mg mL^{-1}, 120 min, 37 °C), derivatized with 70 μL N-methyl-N- (trimethylsilyl) trifluoroacetamide reagent (MSTFA) and incubated (30 min, at 37 °C). The GC–MS analysis was carried with a Thermo Trace Ultra GC equipped with ISQ MS and TriPlus RSH autosampler (Switzerland). Samples (1 μL) was injected and split ratio was 70:1. A TR-5MS capillary column 30 m × 0.25 mm x 0.25 μm was used. Injector temperature was 220 °C ion source 230 °C and the interface 250 °C. Carrier gas flow rate was 1 mL min^{-1}. Temperature program was held at 70 °C for 2 min, then increased to 260 °C (rate 8 °C min^{-1}), where it remained for 18 min, m/z 50–600 was recorded. Peaks were identified according to the mass spectra of known standards or using the NIST 11 and GOLM databases when standards were not available. Experiments were performed using three biological replicates. The detected metabolites were assessed based on the relative response compared to internal standard adonitol and expressed as relative abundance. In addition, the results of metabolites were also expressed as ratio between skin and fruit transformed to log base two as described in detail elsewhere (van den Berg et al., 2006); positive value represent higher abundance in skin and negative value represent lower abundance in skin (Supplementary Table S3).

2.6. Statistical analysis

For physio-chemical data, the statistical analysis was conducted using SPSS (SPSS v21.0., Chicago, USA) by multivariate analysis of variance (MANOVA) statistically significant differences were detected based on post hoc method (Duncan's Multiple Range Test; $P \leq 0.05$) the number of means to be compared. Similarly, the statistical analysis of metabolites and phenolic compounds were conducted using SPSS and statistically significant differences were detected based on Student's t-test; $P \leq 0.05$. Spearman correlation analysis between metabolites and physio-chemical variables was also performed (Supplementary Fig. 1).

3. Results

3.1. The effect of UV-C irradiation on sweet cherries quality

Sweetheart cherry fruit exposed to different UV-C doses times prior to cold storage displayed differences in color parameters after cold period. Particularly, the red color of fruit was deeper as the color indicator C^* and h^0 was decreased in response to 6 kj m^{-2} UV-C treatment compared with control (un-treated) fruits. In addition, skin color becomes darker (lower L* value) after UV-C application either 1.2 or 6.0 kj m^{-2}. As a result, the bright red color of control turned to dark mad red following the highest treatment dose (Fig. 1a, b, c, d).

Skin resistance to penetration was increased significantly by applying UV-C irradiation, approximately by 15% when fruits were treated with 3 and 6 kj m^{-2} (Fig. 2a). On the other hand, traction force for stem removal was unaffected by the different UV-C conditions (data not shown). Notably, respiration rate was declined by 5, 8 and 14% when the fruits were exposed to 1.2, 3.0 and 6.0 kj m^{-2} UV-C irradiation, respectively (Fig. 2b). Ripening index (RI), represented as the ratio of total soluble solids (TSS) to titratable acidity (TA), was enhanced in 6 kj m^{-2} UV-C treated fruit (Fig. 2c), due to the reduction of TA (Fig. 2d).

The physiological disorder fruit surface pitting, expressed as different classes from 0 (no pitting) to 5 (high surface pitting area), was generally reduced by the longest exposure to UV-C illumination (6 kj m^{-2}) (Fig. 3). In this context, a reduction of pitting percentage in class 5 was also observed when fruits treated with 3 kj m^{-2} UV-C. Meanwhile, a strong increase in the number of pitting-free fruits (class 0) was observed following 1.2 and 6.0 kj m^{-2} UV-C application (Fig. 3).

3.2. Impact of UV-C irradiation on biochemical changes

The ratio of biochemical substances between the skin and the whole fruit were altered in response to different UV-C treatments. At the level of skin/fruit ratio, the total phenols were increased after stimulation with 3 and 6 kj m^{-2} UV-C (Fig. 4a). In parallel, skin/fruit ratio of total anthocyanins, tannins, and hydroxycinnamates were also increased in response to all UV-C treatments (Fig. 4c, d, f). Antioxidant capacity as well as flavonoids, expressed as skin/fruit ratio, were also induced by 6 kj m^{-2} UV-C treatment (Fig. 4b, e).

In skin tissue samples, the antioxidant capacity and flavonoids levels were increased following 6 kj m^{-2} UV-C application by 75 and 70%, respectively. In addition, the total skin anthocyanins were induced by 3 and 6 kj m^{-2} UV-C treatments (Supplementary Table S1). By contrast to results obtained in skin tissues, the analysis of the whole cherries fruit samples revealed no differences in the biochemical parameters tested among the applied UV-C treatments (Supplementary Table S1).

Significant changes in pectin status due to 6 kj m^{-2} UV-C exposure was detected in the skin tissue. Indeed, total pectin as well as water-soluble and -insoluble pectin fractions were increased in UV-C treated skin samples (Fig. 5a, b, c); however, the ratio of soluble to insoluble pectin was decreased (Fig. 5d), indicating the higher abundance of insoluble pectin in skin tissue after UV-C treatment (Fig. 5, Supplementary Table S2).

3.3. Metabolite profile in sweet cherry fruit and skin tissue following UV-C irradiation

To characterize the effects of UV-C exposure on sweet cherry fruit metabolism, we determined the changes in primary metabolites in both cherry fruit and skin tissue exposed to 6 kj m^{-2} UV-C. This UV-C dose was selected for metabolic analysis since exhibited the maximal beneficial effects on the physio-biochemical attributes of sweet cherry fruits (Figs. 1–5). A total of fifty-one polar metabolites were quantified in cherry fruit and skin treated with UV-C (Fig. 6). These metabolites correspond to soluble sugars (twelve), sugar alcohols (eight), organic acids (ten), amino acids (fourteen) and others (seven). It is notable that seven (three decreased and four increased) and seventeen (eight decreased and nine increased) metabolites were differentiated due to UV-C exposure in skin and the whole fruit, respectively as compared with the control fruits (Fig. 6, Supplementary Table S3). Furthermore, the ratio of skin to whole fruit metabolites revealed that ten of them were differentiated (seven decreased and three increased) in response to high dose UV-C application (Fig. 6, Supplementary Table S3).

The present analysis disclosed some distinct UV-derived changes between whole fruit and skin samples. For example, we observed lower abundance of mannose and higher of maltotriose (soluble sugars) in fruits treated with 6 kj m^{-2} UV-C (Fig. 6; Supplementary Table S3). In

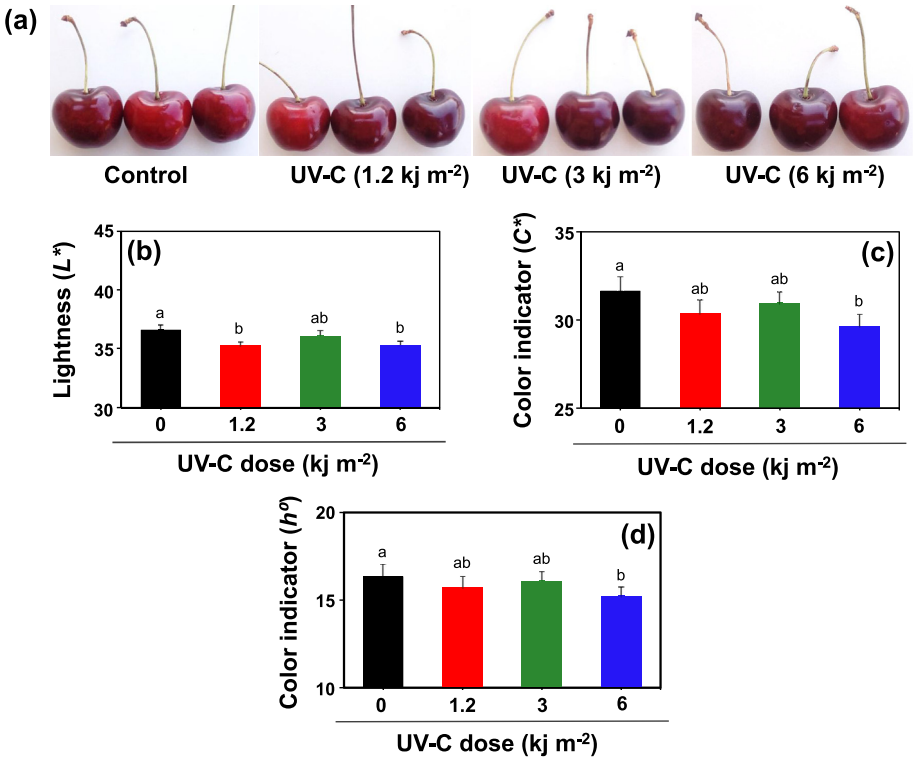

Fig. 1. Phenotype (a) and color parameters; lightness (L^*) (b) and color indicators chroma (C^*) (c) and hue angle (h^o) (d) of sweet cherry 'Sweetheart' exposed to UV-C treatments (1.2, 3.0 or 6.0 kJ m^{-2}) and then cold stored for 10 days. Each value represents the mean of 30 replications per fruit and vertical bars represent standard error of mean (SE). Different letters indicate significant differences among treatments according to Duncan's multiple range test; $P \leq 0.05$. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

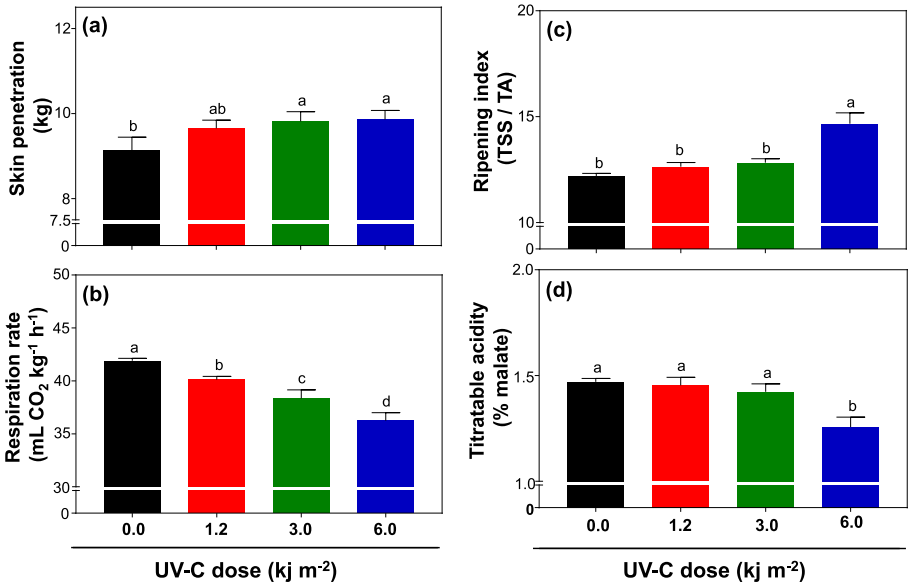

Fig. 2. Skin resistance to penetration (a), respiration rate (b), ripening index (c) and titratable acidity (d) in sweet cherry fruit exposed to UV-C treatments (1.2, 3.0 or 6.0 kJ m^{-2}) and then cold stored. Each value represents the mean of 30 replications per fruit (a) or 3 replications of 10 fruits (b), (c) and (d). Vertical bars represent SE. Different letters indicate significant differences among treatments according to Duncan's multiple range test; $P \leq 0.05$.

whole fruit samples, decrease in two sugars, namely fructose and glucose, was observed in response to UV-C treatment. Furthermore, UV-C decreased glycerol, mannitol and inositol at the whole fruit level. Succinate, galactarate and galacturonate (organic acids) as well as threonine and aspartate (amino acids) were increased in fruit challenged with UV-C application. Also, shikimate in cherry skin together with gluconate and threonate in whole fruit were depressed by UV-C. On the other hand, malate was decreased in both skin and fruit tissue treated with UV-C. Both skin and whole fruit samples had a higher content of asparagine, glutamine and oxoproline (amino acids) and phosphoric acid (other compound) in UV-C treated samples than the control (Fig. 6, Supplementary Table S3).

The metabolic changes between skin and fruit revealed significant difference for thirty and thirty-nine metabolites in control and UV-C fruit, respectively (Supplementary Table S3). Thirty metabolites were commonly identified in both control and UV-C samples. Compared with skin UV-C samples, the levels of rhamnose, mannose, galactarate, threonate and aspartate were increased in the whole fruit UV-C samples. Finally, a set of metabolites, including maltotriose, isoleucine, tyrosine and phospharate, was increased in UV-C treated skin compared to whole fruit samples (Supplementary Table S3). Correlation between metabolites of skin and physio-biochemical attributes indicated a strong negative correlation between two acids (malic acid and ascorbic acid) and pitting class 0, as well as between respiration rate and pitting class 0 (Supplementary Fig. 1).

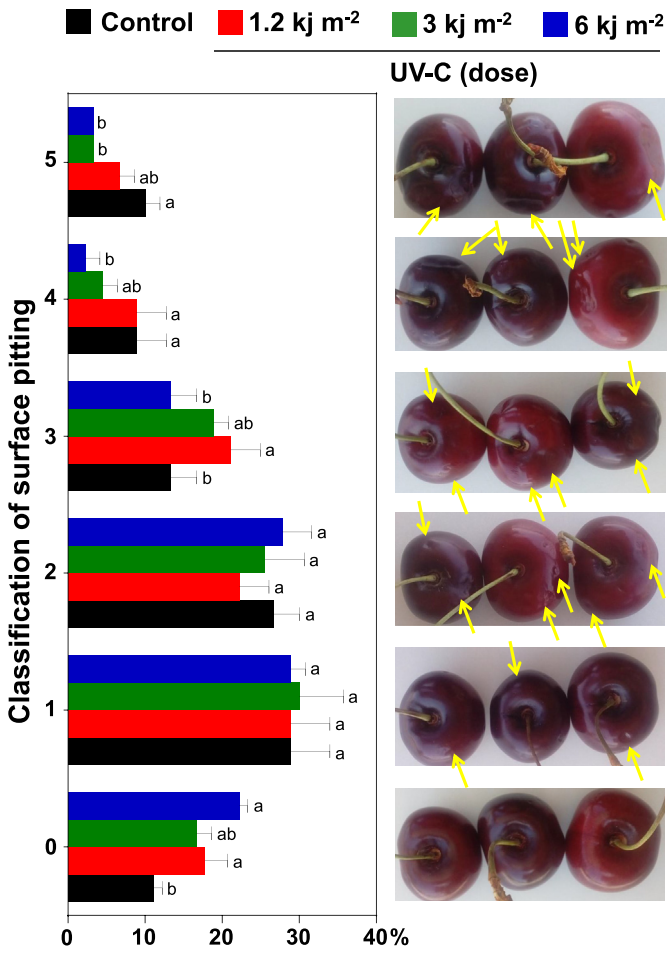

Fig. 3. The classification of surface pitting and representative phenotype of sweet cherry fruit exposed to UV-C treatments (1.2, 3.0 or 6.0 kJ m^{-2}) and then cold stored. Fruits classified to class 0 (no pitting); to class 1 exhibited surface pitting area < 0.1 cm^2; to class 2 exhibited surface pitting area < 0.3 cm^2; to class 3 exhibited surface pitting area < 0.6 cm^2; to class 4 exhibited surface pitting area < 1 cm^2; to class 5 exhibited surface pitting area ≥1 cm^2. Each value represents the mean of 3 replications of 50 fruits and vertical bars represent SE. Different letters indicate significant differences among treatments according to Duncan's multiple range test; P ≤ 0.05.

4. Discussion

Sweet cherries generally characterized by short harvest period and marketing window, however the increasing global production and trade in sweet cherry fruit, impose the need for maintaining and improving cherry fruit quality during longer storage and marketing times (Chockchaisawasdee et al., 2016). The use of UV-C radiation as a postharvest elicitor of beneficial responses in fruit has become a key area of interest (Lu et al., 1991; Gonzalez-Aguilar et al., 2004; González-Aguilar et al., 2007; Pérez-Ambrocio et al., 2018; Sheng et al., 2018; Xu et al., 2019a). However, the mechanisms by which UV-C acts in sweet cherry fruit biology remains unclear.

Postharvest metabolic changes leading to increased respiratory activity, fruit discoloration and softening are key aspects that determine the storage life and quality of fruits (Karagiannis et al., 2018b; Aghdam et al., 2019). Current data indicated that sweet cherry fruit during postharvest period became darker, as evidenced by the reduction of color indicators C^*, h^0 and L^*, following the increasing exposure to UV-C from 1.2 to 6 kj m^{-2}. Such fruit discoloration due to UV-C irradiation was also observed in tomato (Liu et al., 2009) as well as at persimmon and cucumber (Imaizumi et al., 2018) and has been associated with an increased level of tannins and a decreased level of carotenoids, thus affecting the color of the fruits (Bu et al., 2014; Imaizumi et al., 2018).

An interesting finding that emerged from this work is the fact that ultraviolet treatments result in higher firmness and lower respiration rate, suggesting that UV-C has an important role in the delay of cherry senescence process after cold storage. Previous studies indicate that postharvest UV-C action is associated with inhibition of respiration due to the decrease of the activity of the respiratory enzymes of succinic dehydrogenase and cytochrome C oxidase of the inner mitochondrial membrane in ripen peach fruit (Yang et al., 2014). Moreover, ripening index was increased by prolonged UV-C treatment, mainly due to the fact that acidity was decreased, while TSS remained unchanged (data not shown). Similar results were noticed in strawberry, tomato and persimmon (Cote et al., 2013; Khademi et al., 2013) highlighting the impact of UV-C irradiation in the reduction of acidity of red-colored fruits.

Mechanical injury of sweet cherry fruit causes the disorder surface pitting, in which skin depressions overlie necrotic lesions in the fleshy mesocarp (Wade and Bain, 1980). Storage at temperatures near 0 °C or the transfer of fruit from cool storage to room temperature worse the disorder (Wade and Bain, 1980). Here, we observed that pitting hallmarks of sweet cherry fruit were notably alleviated by UV-C application. In a recent study, the examined cherry cultivar 'Sweetheart' has been classified as susceptible to mechanical damage and surface pitting (Param and Zoffoli, 2016). It has been suggested that critical factor having a major influence on the susceptibility of this cultivar to pitting is the alcohol insoluble residue which constitutes mainly the cell-wall material (Param and Zoffoli, 2016). In this regard, another interesting observation from this work was the fact that total pectins and their fractions (water-soluble and -insoluble pectin) in the cherry skin tissue were negatively associated with pitting, as the stimulation of their steady-state level by 6 kj m^{-2} UV-C application was accompanied by a reduction of pitting.

The current analysis revealed that the impact of UV-C on the whole fruit was relative negligible compared with the effect on the skin samples, suggesting that the UV-C application target their effects mainly to skin's barrier layer of fruit rather than the inside body of cherry fruit. This is the fact that UV-C does not penetrate in depth fruit tissues, as being blocked by UV filtering compounds and the action of UV-C is limited to the first cell layers (Guerrero-Beltrán and Barbosa-Cánovas, 2004). Particularly, it is indicated that several oxidative-related features of the sweet cherry skin, such as antioxidant capacity, anthocyanins, total phenols and flavonoids were increased following high UV-C exposure. Activation of secondary metabolism and biosynthesis of antioxidants due to plant tissue exposure to ultraviolet irradiation has been reported in previous studies (Liu et al., 2018; Pérez-Ambrocio et al., 2018; Sheng et al., 2018). For example, UV-C has been related to the regulation and biosynthesis of key enzymes in the biosynthetic route of flavonoids such as phenylalanine ammonia lyase (PAL) and chalcone synthase (CHS) (Zoratti et al., 2014). Possibly, such a response is connected to the important role of flavonoids as photoprotectors; having both antioxidant and UV-screening properties (Agati and Tattini, 2010), and therefore may contribute to the prevention of UV stress in sweet cherry fruit following cold storage. Interestingly, the exposure of sweet cherry to UV-C and then to cold stress may collectively increase the level of oxidative stress more than compared to UV-C application only. Thus, it can be assumed that secondary metabolites and antioxidants may act as potent site-specific antiradicals that quickly neutralize cherry skin tissue damage by UV-C and cold-originated oxidative stress, possibly also resulting in increased resistance against pitting.

The lower respiration rates of cherries treated with UV-C suggests that the fruit has lower physiological activity and moderate metabolic activity. To explore this phenomenon, we employed metabolomic analysis to characterize the metabolic activity in cherry tissues at an early stage of fruit senescence. Additionally, we identified metabolic networks that differed in control and UV-C treated fruit while also

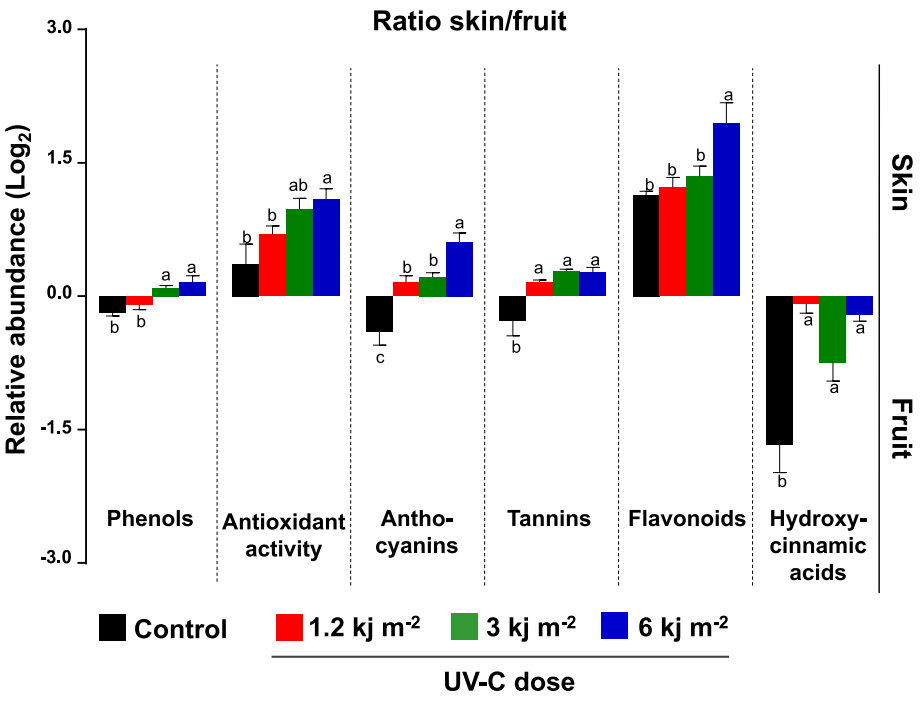

Fig. 4. Biochemical traits expressed as a relative abundance of the ratio skin/whole fruit samples. Total phenols (a), antioxidant capacity (b), total anthocyanins (c), tannins (d), flavonoids (e), and hydroxycinnamic acids (f) of sweet cherry fruit exposed to UV-C treatments (1.2, 3.0 or 6.0 kJ m^{-2}) and then cold stored. Each value represents the mean of 3 replications of 10 fruits and vertical bars represent SE. Different letters indicate significant differences among treatments according to Duncan's multiple range test; $P \leq 0.05$.

being expressed in both skin and whole fruit level (Fig. 7). For instance, galacturonate was increased in skin and in whole fruit samples with prolonged UV-C irradiation (Fig. 7). It is well established that total pectin fractions consist mainly of galacturonate and other polyuronides while across fruit ripening and senescence, total pectin declined and solubilized to soluble polyuronides and carbohydrates (Ali et al., 2004). A similar scenario is being proposed in this study since it is observed that UV-C provokes the increment of pectin fractions and galacturonate with a concomitant reduction in fruit soluble sugars, such as glucose and fructose (Fig. 7). In tomato fruit, postharvest application of UV-C suppressed the expression of cell wall related genes and key genes of primary metabolism, like myo-inositol-1-phosphate synthase that could regulate the abundance of inositol (Liu et al., 2011), which in turn participates along with galacturonate in ascorbate biosynthesis (Ishikawa et al., 2006). It is also remarkable that skin resistance to penetration of sweet cherry was linked with total pectin level (Fig. 7). Previously, it has been demonstrated that UV-C prevents softening of cherry tomato fruit by reducing the degradation of insoluble pectin fractions as well as by the suppression of major cell wall degrading enzymes (Bu et al., 2013).

Since malic acid is the main acid in cherry fruit (Michailidis et al., 2017), conditions which result in its decline lead also to a simultaneous reduction in the acidity of sweet cherry (Fig. 7). In addition, UV illumination could be considered as a dehydration factor for the exposed tissues due to high energy release on fruit surface, thus contributing to the mobilization and diffusion of water molecules into environment (Tunçal and Uslu, 2014). It has been reported that organic acids in berries under the effect of dehydration were degradated by the activation of malate dehydrogenases (Conde et al., 2018). Such a mechanism is plausible in cherry fruit since we observed that malate was decreased both in skin and fruit samples, reinforcing the hypothesis that UV-C induced dehydration in fruits. Meanwhile, several amino acids, including glutamine and asparagine were accumulated in response to UV-C in both skin tissue and whole fruit level, indicating a possible UV-specific metabolic adjustment. An induction of asparagine and glutamine contents were also observed in various fruits that have experienced stressful conditions (Keutgen and Pawelzik, 2008; Yun et al., 2015; Ainalidou et al., 2016; Tanou et al., 2017; Karagiannis et al.,

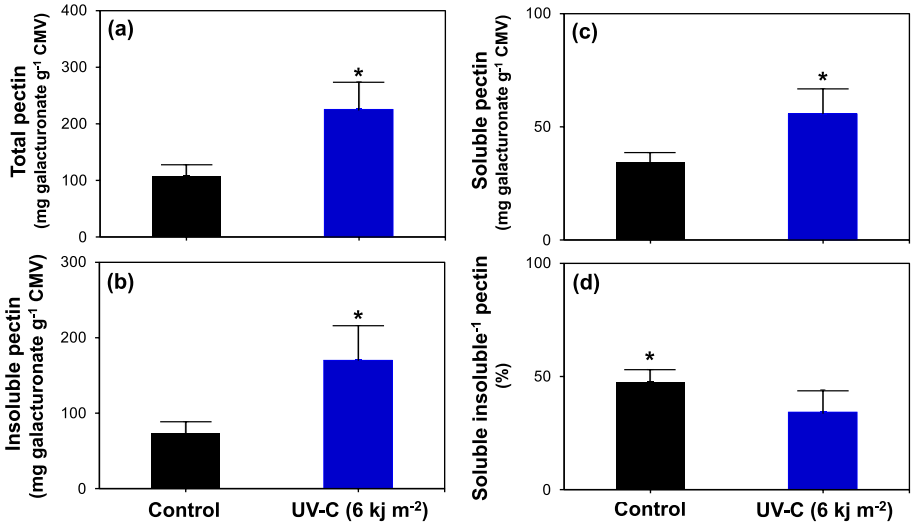

Fig. 5. Skin-derived total pectin (a), insoluble pectin (b), soluble pectin (c) and ratio soluble insoluble^{-1} pectin (d) in sweet cherry fruit exposed to 6.0 kJ m^{-2} UV-C illumination. Each value represents the mean of 3 replications of 30 fruits and vertical bars represent SD. Asterisk indicate significant differences between control and 6 kj m^{-2} UV-C treatment according to Student t-test; $P \leq 0.05$.

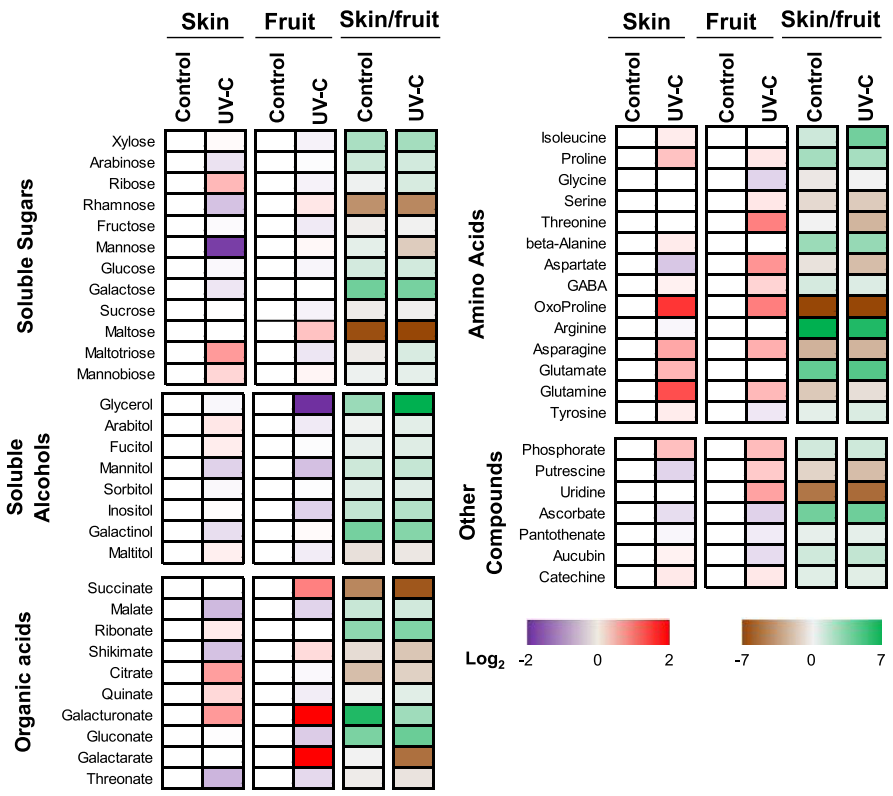

Fig. 6. Heat map of primary metabolites measured in the skin, whole fruit and the ratio of skin/whole fruit of 'Sweetheart' sweet cherry exposed to UV-C illumination (6 kj m^{-2}). Increase is indicated in red (skin and fruit) or green (ratio between skin and fruit; skin $fruit^{-1}$); decrease is indicated in purple (skin and fruit) or brown (ratio between skin and fruit; skin $fruit^{-1}$) (see color scale). Metabolites are expressed as relative abundance compared to internal standard adonitol. Data are provided in Supplementary Table S3. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

2018b), indicating the connection of these two metabolites with stress, such as induced by UV-C (Fig. 7).

The present study showed that the accumulation level of oxoproline (5-oxoproline also called pyroglutamic acid) was strongly induced by UV-C. Oxoproline is a non-protein amino-acid derivative synthesized when glutamic acid or glutamine are cyclized as lactam. Although the exact role of oxoproline in plants remains uncertain, the proposed functions of oxoproline include its role as an osmoprotectant (Slama et al., 2015). Thus, the possibility that UV-C promoted oxoproline accumulation under UV-driven dehydration stress, probably to counteract the osmotic pressure induced by water deficit cannot be excluded. However, being a glutamine analogue and a potential reserve of glutamine, oxoproline is strongly linked to all processes involving glutamine. Given also that the glutamine was induced by UV-C in the skin samples we hypothesize that the UV-stimulated the accumulation of both oxoproline and glutamine could act as a signaling mechanism under UV-C stress conditions. In addition to its role as a metabolic fuel, glutamine may enhance many cell functions via the activation of various transcription factors and activation of these transcription factors may amplify glutamine signaling in plants, notably under stress conditions (Kan et al., 2015).

Fructose and glucose are the main reducing sugars in sweet cherry fruit at harvest as well as during post-harvest period (Michailidis et al., 2017). In line with previous studies (Charles et al., 2016; Lin et al., 2017), a reduction of fructose and glucose in whole fruits exposed to UV-C irradiation was measured (Fig. 7, Supplementary Table S3). In whole cherry fruit, UV-C irradiation also depressed the levels of gluconate and glycerol that participate in carbon metabolism via pentose phosphate pathway (PPP). The PPP has gained recognition as being a central player in reducing power mechanism, and in controlling and maintaining cell redox homeostasis. As such, it has been implicated in several oxidative stress-related conditions in various cellular mechanisms (Krüger et al., 2011; Riganti et al., 2012; Minas et al., 2014; Tanou et al., 2015). Hence, it is anticipated that during UV-C exposure, a significant adjustment takes place to counter oxidative damage by adapting an energy-efficient response system in the sweet cherry fruit. In parallel, the tissues of UV-C treated fruits show higher antioxidant capacity, anthocyanins and flavonoids. Such a feature gives in UV-C stimulus prior to cold storage stress imposition a strict resemblance to a beneficial characteristic (i.e the stimulation of plant response by low levels of inhibitors or stress), especially in terms of antioxidant-based responses.

5. Conclusion

These findings suggest that UV-C delayed several ripening features of sweet cherry following cold storage, indicating that it could maintain postharvest fruit quality. A reduction of the physiological disorder, skin pitting, in response due to UV-C application was also observed. Also, UV-C inhibited pectin degradation and delayed the loss of resistance to penetration by the skin thus contributed to the firmness maintenance. Treatments with UV-C stimulated antioxidants capacity and bioactive compounds, like flavonoids and phenolics. The depression of respiration in fruit exposed to UV-C was accompanied with the alternation of several metabolites. In whole fruit samples, UV-C induced the accumulation of several amino acids, including threonine and aspartate while depressed the amounts of various sugars, such as glucose and fructose as well as several alcohols (e.g., inositol, glycerol and mannitol). In skin samples, several metabolites, such as mannose, malate, galacturonate, oxoproline glutamine, asparagine and were altered by UV-C. Finally, we observed significant differences in the abundance of some metabolites (eg., mannose, glycerol) between fruit skin and whole fruit. These findings will improve our understanding of the key processes involved in UV-C action mode in the modulation of postharvest fruit biology.

Conflicts of interest

The authors declare no conflicts of interest.

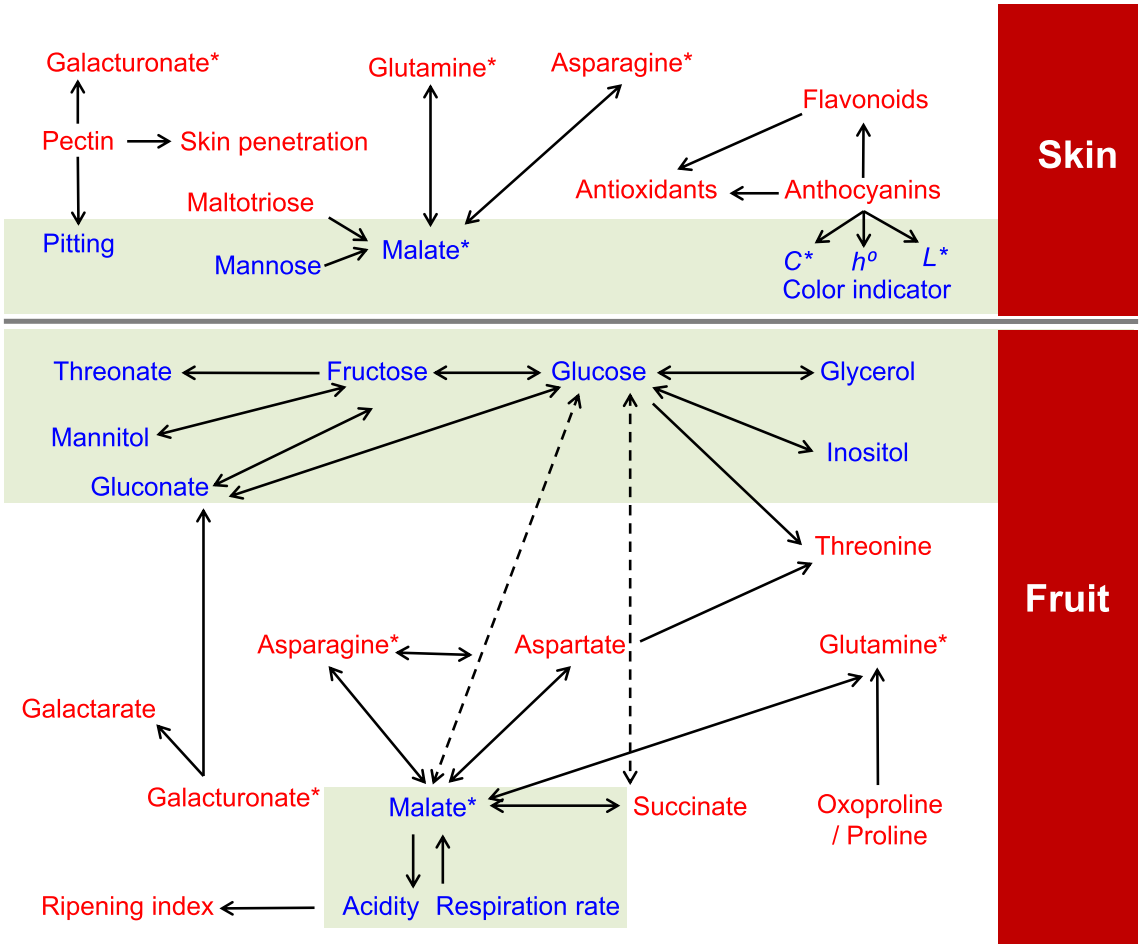

Fig. 7. A schematic model illustrating how UV-C could altered sweet cherry 'Sweetheart' physio-biochemical and metabolic characteristics in both skin tissue and whole fruit level. Increase is indicated with red; decrease is indicated with blue. Significant difference of metabolites between control and UV 6 kj m^{-2} treatment tested based on Student t-test; Physio-biochemical differences tested according to Duncan's multiple range test; $P \leq 0.05$. An asterisk (*) denote common response (increase/decrease) in skin and whole fruit samples. Data are provided in Supplementary Table S1, S2 and S3. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Author contributions

A. Molassiotis and M. Michailidis designed the experiment, M. Michailidis analyzed the data and wrote the first draft manuscript, E. Karagiannis, C. Polychroniadou, G. Tanou, and K. Karamanoli, accomplished the laboratory analyses and helped in data/draft manuscript processing.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.plaphy.2019.09.030.

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