



# Postharvest UV-C Irradiation Influenced Cellular Structure, Jasmonic Acid Accumulation, and Resistance Against Green Mold Decay in Satsuma Mandarin Fruit (*Citrus unshiu*)

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Green mold caused by *Penicillium digitatum* is an important factor limiting the shelf life of mandarin fruit. In this study, the effect of ultraviolet-C (UV-C) irradiation on cellular structure, endogenous jasmonic acid (JA), and development of *P. digitatum* in satsuma mandarin fruit was investigated. UV-C treatments included 0 (untreated control), 3, and 10 kJ m<sup>-2</sup> or the exposure time of 0, 1.18, and 4.52 min, respectively. The UV-C dose of 10 kJ m<sup>-2</sup> significantly reduced the development of *P. digitatum* both *in vitro* and *in vivo*, resulting in the maintenance of the cellular structure of the albedo tissue. The production of malondialdehyde (MDA) was decreased upon UV-C treatment of 10 kJ m<sup>-2</sup>. The concentration of JA increased in the treatment of 10 kJ m<sup>-2</sup> compared to the treatment of 3 kJ m<sup>-2</sup> and the control. UV-C irradiation increased total phenolic and total flavonoid concentrations and DPPH radical scavenging capacity. These results suggest that UV-C at 10 kJ m<sup>-2</sup> has a potential to control green mold caused by *P. digitatum*, maintain cellular structure, stimulate the accumulation of JA, and induce biochemical compounds in satsuma mandarin.

**Keywords:** green mold, cellular structure, jasmonic acid, mandarin fruit, UV-C radiation

## INTRODUCTION

Citrus fruit is one of the largest commodities consumed worldwide (Lu et al., 2020). Satsuma mandarin (*Citrus unshiu*) is one of the most popular fruit for fresh consumption at present because it is seedless, is rich in bioactive compounds, and contributes to nutrition and energy sources for health (Gao et al., 2018). However, this citrus fruit is highly susceptible to postharvest decay caused by various pathogens such as *Botrytis cinerea*, *Penicillium italicum*, and *Penicillium digitatum*. In general, green mold decay caused by the pathogenic fungus *P. digitatum* is the major cause of postharvest losses in mandarin fruit. The fungus causes a soft water-soaked peel that is later covered with white mycelia of the fungus (Chen and Peng, 2016).

Generally, fungicides have been used to suppress decay in citrus before harvest (Yamaga et al., 2016). However, the frequent use of some fungicides has led to adverse effects on human health and the environment, as well as the development of fungicide-resistant pathogens. For example, *P. digitatum* was resistant to thiabendazole due to a mutation of  $\beta$ -tubulin gene correlating to amino acid 200 (Sánchez-Torres and Tuset, 2011). Recently, several studies have used ultraviolet-C (UV-C) irradiation to control microbial infections in fruits and vegetables (Mohamed et al., 2017; Sripong et al., 2019). For example, irradiation with UV-C reduced gray mold development caused by *B. cinerea* in strawberry fruit (*Fragaria ananassa*) (Jin et al., 2017), and regulated gene expression related to lipid oxidation and cell wall degradation in tomato fruit (*Lycopersicon esculentum*) (Liu et al., 2011). Moreover, in fresh produce exposed to UV-C irradiation, antioxidant capacity such as total phenolic and total flavonoid concentrations were stimulated (Park and Kim, 2015).

Jasmonic acid (JA), an endogenous plant hormone, is usually produced in plants in response to various stressful situations (Yang et al., 2019a). Studies have reported that JA influence the direct and indirect response to trigger signaling molecules that then activate the plant stress tolerance (Zhang et al., 2009; Margherita et al., 2018). This hormone plays a role in increasing the production of secondary metabolites and defense strategies against pathogens in plants (Shikano et al., 2018).

Therefore, the objective of this study was to investigate the effect of UV-C irradiation on cellular structure, concentrations of JA and bioactive compounds, antioxidant capacity, and green mold development in satsuma mandarin during storage.

## MATERIALS AND METHODS

### Suppression of Fungal Development Caused by *Penicillium digitatum*: In vitro Study

A-7-day-old pure culture of *P. digitatum* (Registration No. MAFF 242809) was used in this study. The mycelial disk, 6 mm in diameter, was placed on the center of potato dextrose agar (PDA) in a Petri dish. The dishes were uncovered just before being placed in the UV-C chamber and placed 25 cm away from the UV-C sources with the critical peak emission at 253 nm (GL-20, Toshiba, Japan). Three groups of 10 plates were exposed to 3 UV-C doses of 0 (control), 3, and 10 kJ m<sup>-2</sup> or the exposure time of 0, 1.18, and 4.52 min, respectively. After UV-C treatment, the plates were covered and then incubated at 25°C. The effect of UV-C treatments on the development of *P. digitatum* was examined at 3, 4, and 5 days after treatment (DAT), which was calculated from the longest length and the greatest width perpendicular to the length of the mycelium using a transparent ruler.

### Inhibition of *Penicillium digitatum* in Satsuma Mandarin Fruit

“Aoshima unshu” satsuma mandarin (*C. unshiu*) fruit at commercial maturity stage were harvested in late December from the orchard in Shizuoka Prefecture, Japan. Prior to treatment, fruits were disinfected by immersion in 150 ppm sodium

hypochlorite (NaOCl) for 1 min, rinsed thoroughly in tap water, and drained overnight at 25°C. Satsuma mandarin fruits were divided into three groups (90 fruits per treatment). Sufficient spores from a pure culture of *P. digitatum* were harvested using 25 ml of sterilized distilled water containing 0.5% agar and then adjusted to a final spore concentration of 1.2 × 10<sup>6</sup> spores ml<sup>-1</sup>.

For inoculation, a wound of 5-mm diameter and 3-mm depth was made between the vertical and horizontal parts at the equator of the fruit using a sterilized scalpel (Suktawee et al., 2019). The 20 ml of spore suspension was inoculated into the center of the wound of each fruit using a micropipette and allowed to air-drain for pathogen settlement. Two groups of artificially infected fruits were irradiated with UV-C at different irradiation doses of 3 and 10 kJ m<sup>-2</sup>, and the non-irradiated group was set as untreated control. All fruits were stored at 25°C and 95% relative humidity. Lesion diameters of green mold infestation (15 fruits per treatment) were measured and calculated by taking the mean of the vertical and horizontal of each lesion with a digital vernier caliper at 3, 4, and 5 DAT.

### Effect of UV-C Irradiation on the Mycelial Density of Albedo

Fruit peel before and after inoculation (5DAT) were cut into 0.5 cm<sup>3</sup> and immediately coated with liquid nitrogen. The sample was observed under a scanning electron microscope (SEM) (SU1510; Hitachi, Japan). The images were then illustrated at the accelerating power of 30.0 kV with the magnification of 100 μm.

### Effect of UV-C Irradiation on Lipid Peroxidation

Lipid peroxidation was determined as production of malondialdehyde (MDA) equivalents using a modified method of Phonyiam et al. (2016). The extracted sample (500 μl) was mixed with 0.5% of thiobarbituric acid (TBA) in 10% of trichloroacetic acid (TCA) (1.5 ml). The mixed solution was incubated at 85°C for 30 min. Then, the cooled mixture was measured with a spectrophotometer (U-2910; Hitachi, Japan) at the absorbance of 532 nm. A non-specific turbidity was measured at the absorbance of 600 nm.

### Effect of UV-C Irradiation on JA Concentration

The JA concentration was analyzed according to the method of Kondo et al. (2005) with modifications. Fresh peel sample (1 g) was homogenized in 1 M citric acid (250 μl), sodium chloride (NaCl) (5 ml), and diethyl ether containing 0.005% BHT (10 ml). The sample mixture was then mixed with ibuprofen (500 μl) and used as an internal standard. The diethyl ether fraction was collected after centrifugation at 15,000 g for 10 min at 4°C. Then, the qualification of JA was evaluated by RP-18 octadecylsilyl column (5 μm, 2 mm I.D. × 150 mm; Kanto Chemical, Tokyo, Japan). The JA concentration was calculated from the ratio of the peak area for *m/z* 206/161 (ibuprofen) and expressed as nanomole per 1 kg of fruit weight (nmol kg<sup>-1</sup> FW).

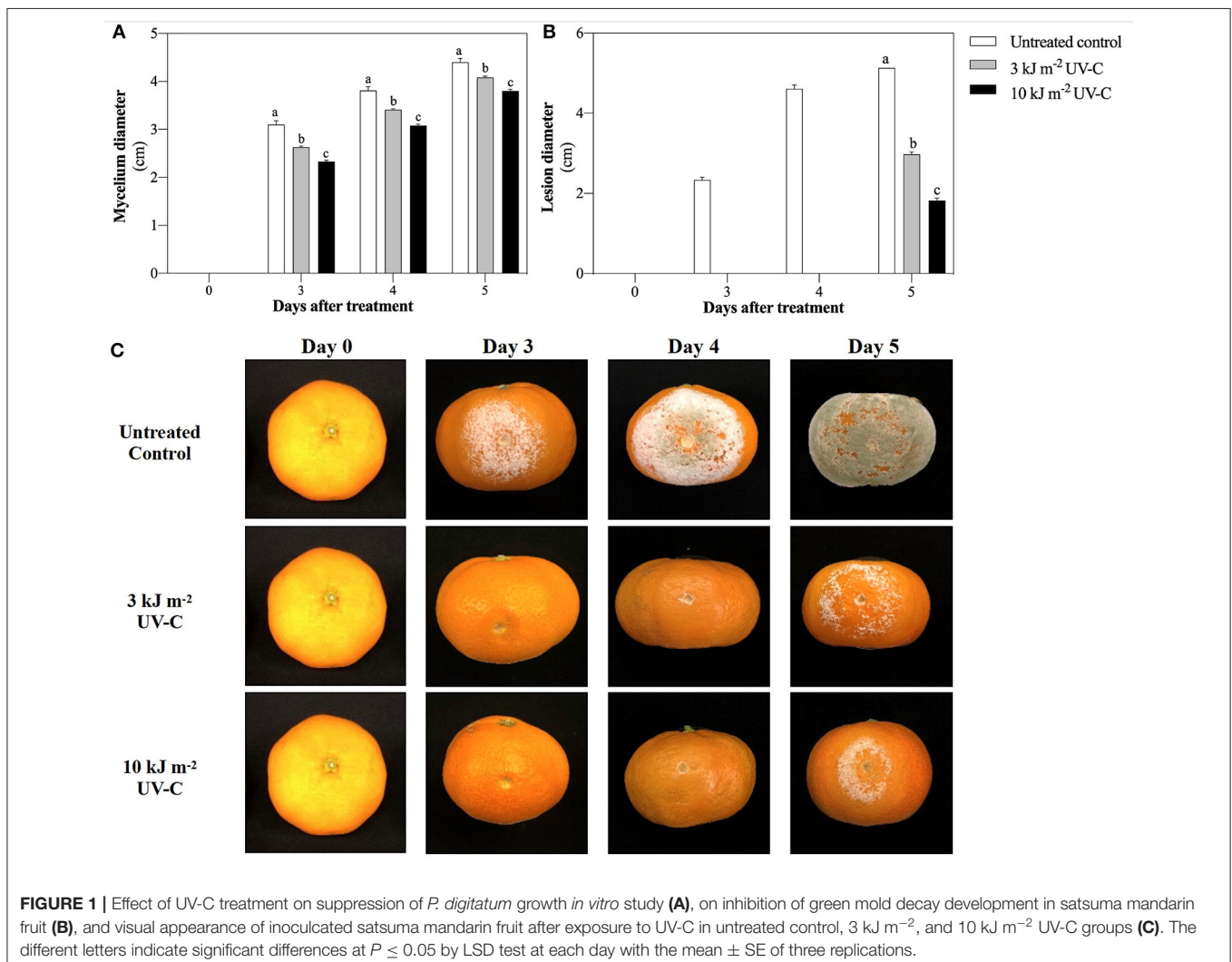
## Effect of UV-C Irradiation on Bioactive Compounds and Antioxidant Capacity

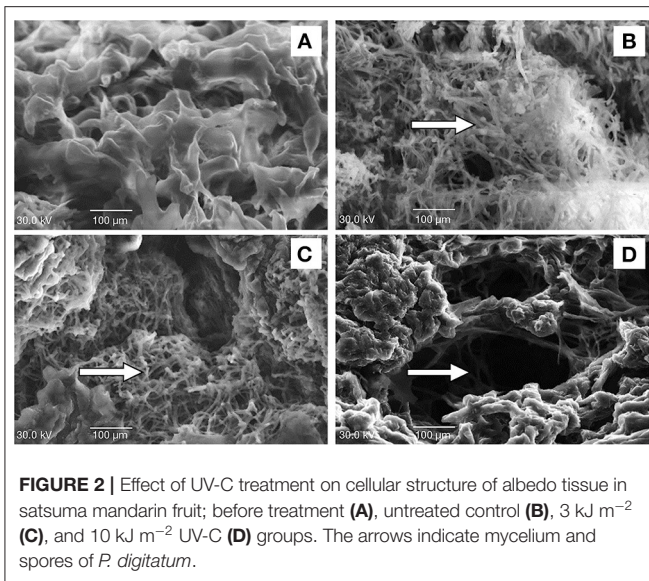
Peel sample (3 g of fresh weight) was homogenized in 20 ml of 80% methanol. The homogenized samples were then centrifuged at 15,000 g for 10 min at 4°C. Total phenolic concentrations in peel were analyzed using a spectrophotometer (U-2910; Hitachi, Japan) according to the Folin–Ciocalteu assay of Sheng et al. (2018) with slight modifications. The 0.25 ml of the crude extract was mixed with 1.25 ml of 10% Folin–Ciocalteu reagent and 1 ml of 7.5% sodium carbonate ( $\text{Na}_2\text{CO}_3$ ). The mixture was incubated for 1 h at ambient condition, and the total phenolic concentration was measured at the absorbance of 765 nm and expressed as milligram of gallic acid equivalent (GAE) per 1 kg of fruit weight ( $\text{mg GAE kg}^{-1}$  FW). Total flavonoid concentration was measured by the method modified from Sheng et al. (2018). The sample (250  $\mu\text{l}$ ) was mixed with 75  $\mu\text{l}$  of 10% aluminum chloride ( $\text{AlCl}_3$ ), 75  $\mu\text{l}$  of 5% sodium nitrite ( $\text{NaNO}_2$ ), and 1 ml of deionized water. After 5 min, 1 ml of 4% sodium hydroxide ( $\text{NaOH}$ ) was added to the mixture and incubated for 10 min

at ambient temperature. The reaction mixture was evaluated at the absorbance of 510 nm. Total flavonoid concentration in the peel sample was expressed as mg catechin equivalent (CAE) per 1 kg of fruit weight ( $\text{mg CAE kg}^{-1}$  FW). The DPPH radical scavenging capacity was determined according to the method described by Phonyiam et al. (2016) with some modifications. The sample extract (500  $\mu\text{l}$ ; 9 replicates per treatment) was mixed with 0.1 mM of DPPH-methanolic solution (1.5 ml) and the mixture was incubated. After incubation at 25°C for 30 min, DPPH radical scavenging capacity was monitored at the absorbance of 517 nm and expressed as micromole Trolox equivalent (TE) 1 kg of fruit weight ( $\mu\text{mol TE kg}^{-1}$  FW).

## Statistical Analysis

Triplicate determinations were analyzed for the entire duration of the experimental period using the least significant difference (LSD) test at the significance level of  $P \leq 0.05$  (SPSS 16; IBM, Armonk, NY). Data were expressed as the mean  $\pm$  standard error (SE).





**FIGURE 2 |** Effect of UV-C treatment on cellular structure of albedo tissue in satsuma mandarin fruit; before treatment (A), untreated control (B), 3 kJ m<sup>-2</sup> (C), and 10 kJ m<sup>-2</sup> UV-C (D) groups. The arrows indicate mycelium and spores of *P. digitatum*.

## RESULTS

### Green Mold Development

Mycelial growth of *P. digitatum* was significantly lower in the UV-C treatments than that in the control (Figure 1A). At 5 DAT, mycelium diameters were  $3.80 \pm 0.04$ ,  $4.08 \pm 0.03$ , and  $4.40 \pm 0.08$  cm in the UV-C treatments of 10, 3, and 0 kJ m<sup>-2</sup> (control), respectively. This indicates that UV-C irradiation suppresses *in vitro* growth of *P. digitatum*. Similarly, mandarin fruit treated with 10 kJ m<sup>-2</sup> showed the smallest lesion diameter ( $1.82 \pm 0.06$  cm) compared to those treated with 3 kJ m<sup>-2</sup> ( $2.97 \pm 0.06$  cm) and the controls ( $5.13 \pm 0.00$  cm) (Figure 1B). The effect of UV-C irradiation on green mold development on mandarin is shown in Figure 1C. Furthermore, UV-C at a dose of 10 kJ m<sup>-2</sup> significantly promoted the suppression of mycelial density while maintaining the albedo tissue of cellular structure on 5 DAT compared to other treatments (Figure 2).

### Lipid Peroxidation

MDA concentrations in all treatments increased slightly from 3 DAT to 4 DAT and then decreased at 5 DAT (Figure 3). At 4 DAT, all UV-C doses inhibited MDA concentrations, as indicated by the significantly lower MDA concentrations in the UV-C treatments ( $22.90 \pm 1.02$  and  $27.47 \pm 0.50$  mmol kg<sup>-1</sup> FW for 10 and 3 kJ m<sup>-2</sup>, respectively) compared with the untreated control ( $39.87 \pm 1.58$  mmol kg<sup>-1</sup> FW). This result suggests that the strongest suppression of MDA was achieved at the UV-C dose of 10 kJ m<sup>-2</sup>.

### JA Concentration

UV-C treatments significantly enhanced JA accumulation in mandarin fruit (Figure 4). In 4 DAT, JA concentration was increased in the UV-C treatment with 10 kJ m<sup>-2</sup> ( $338.33 \pm 6.49$  nmol kg<sup>-1</sup> FW), while in the treatment with 3 kJ m<sup>-2</sup>, it was  $198.37 \pm 14.76$  nmol kg<sup>-1</sup> FW. Among the treatments, the lowest JA concentration was observed in the untreated control.

## Bioactive Compounds and Antioxidant Capacity

The total phenolic concentration of fruits irradiated with UV-C increased significantly. The total phenolic concentration in inoculated fruit after treatment with UV-C at 3 and 10 kJ m<sup>-2</sup> was  $2,539.29 \pm 37.11$  and  $2,502.70 \pm 32.20$  mg GAE kg<sup>-1</sup> FW, respectively, while the total phenolic concentration in the untreated control was  $2,294.42 \pm 20.40$  mg GAE kg<sup>-1</sup> FW (Figure 5A).

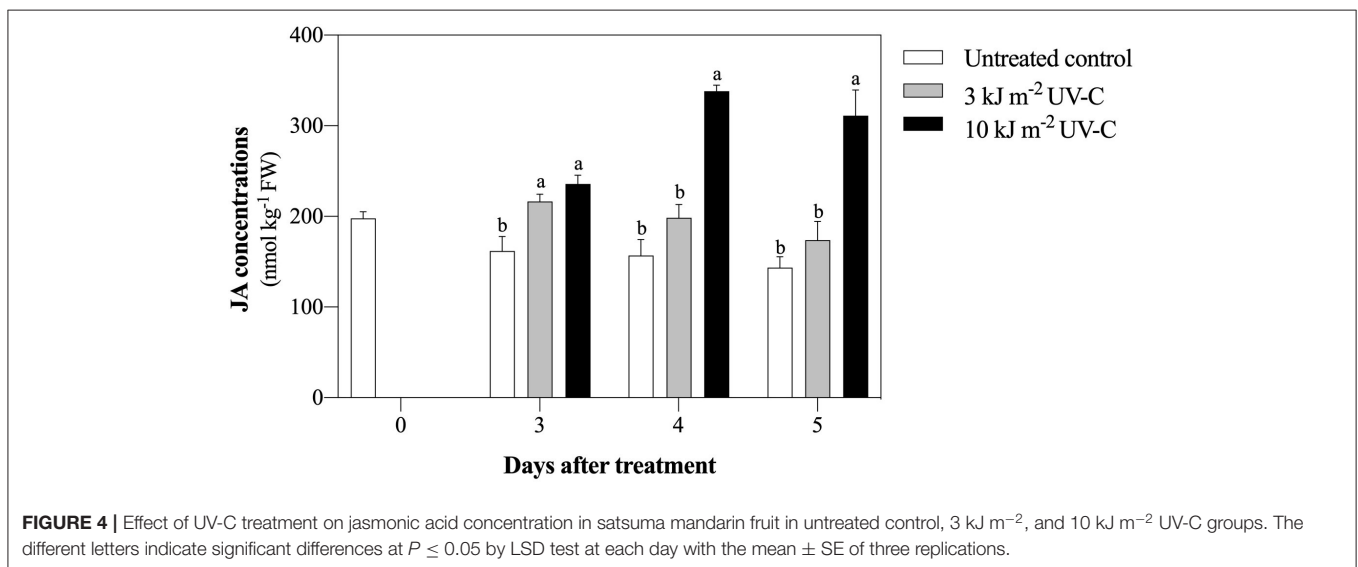
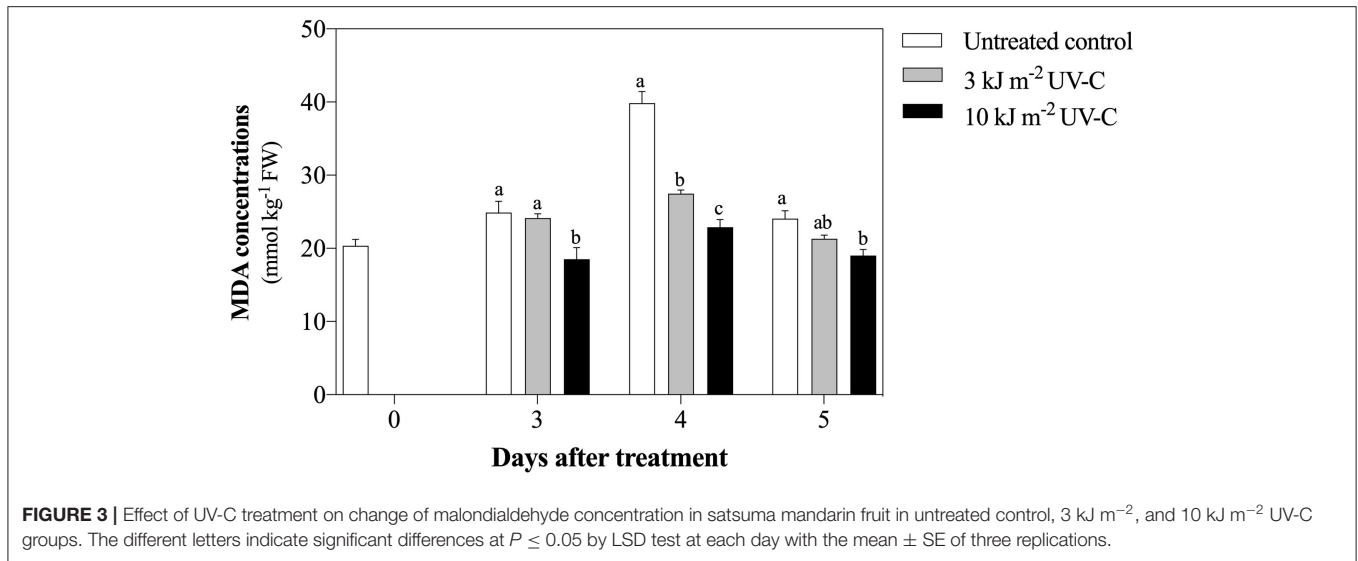
Total flavonoid concentration increased in all treatments at 3 DAT and then decreased until the end of the storage period (Figure 5B). At 5 DAT, the total flavonoid concentration was significantly higher in the UV-C treatment with 10 kJ m<sup>-2</sup> ( $509.99 \pm 7.16$  mg CAE kg<sup>-1</sup> FW) compared with the treatment with 3 kJ m<sup>-2</sup> ( $433.65 \pm 6.90$  mg CAE kg<sup>-1</sup> FW) and the untreated control ( $437.00 \pm 3.14$  mg CAE kg<sup>-1</sup> FW).

At 3 DAT, DPPH scavenging capacity increased significantly in fruit treated with 10 kJ m<sup>-2</sup> UV-C treatments compared with the other treatments (Figure 5C). Moreover, the highest DPPH scavenging capacity was obtained in the 3 kJ m<sup>-2</sup> UV-C treatment at 4 DAT ( $6,343.97 \pm 113.86$  µmol TE kg<sup>-1</sup> FW), while the DPPH values in the 10 kJ m<sup>-2</sup> treatment and the untreated control were  $5,870.30 \pm 116.49$  µmol TE kg<sup>-1</sup> FW and  $5,804.98 \pm 95.68$  µmol TE kg<sup>-1</sup> FW, respectively.

## DISCUSSION

UV-C radiation has been demonstrated to inhibit *Escherichia coli* in apple (*Malus domestica*) (Graça et al., 2013), *Guignardia citricarpa* in orange (*Citrus sinensis*) (Canale et al., 2011), and *Colletotrichum musae* in banana (*Musa acuminata*) (Bokhari et al., 2013). In addition, Oliveira et al. (2016) and Jin et al. (2017) reported that UV-C induces disease resistance response and promotes pathogen-related genes such as *cinnamoyl CoA reductase 1 allele (CCR-1 allele)*, *chitinase 2 (CHI2)*, and *phenylalanine ammonia lyase 6 (PAL6)* in strawberry fruit. In this study, the growth of *P. digitatum*, the causal agent of green mold disease, was significantly lower than that of the untreated control both *in vitro* and *in vivo* upon UV-C treatment of 10 kJ m<sup>-2</sup>. This suggests that UV-C treatment may have a direct effect on the fungus and an indirect effect by inducing defense mechanism against the pathogen infection in satsuma mandarin fruit.

The cell wall is the primary mode of entry of pathogen into plant tissue. The alteration of cell structure barrier could influence the colonization of pathogen (Cantu et al., 2008). Our study indicated that treatment with UV-C at 10 kJ m<sup>-2</sup> greatly reduced fungal mycelia and maintained the cellular structure of the albedo tissue in infected satsuma mandarin fruit. This result is in agreement with a previous study that showed that high dose of UV-C may have induced the plasmolysis process of epidermal cells, resulting in the strengthening of cell wall structure (Charles et al., 2008). However, UV-C at 3 kJ m<sup>-2</sup> and the untreated control at 5 DAT showed intense mycelia of *P. digitatum*. Therefore, the result suggests that 10 kJ m<sup>-2</sup> UV-C induces disease resistance by improving the structural barrier of the cell wall, resulting in inhibition of green mold infestation. On

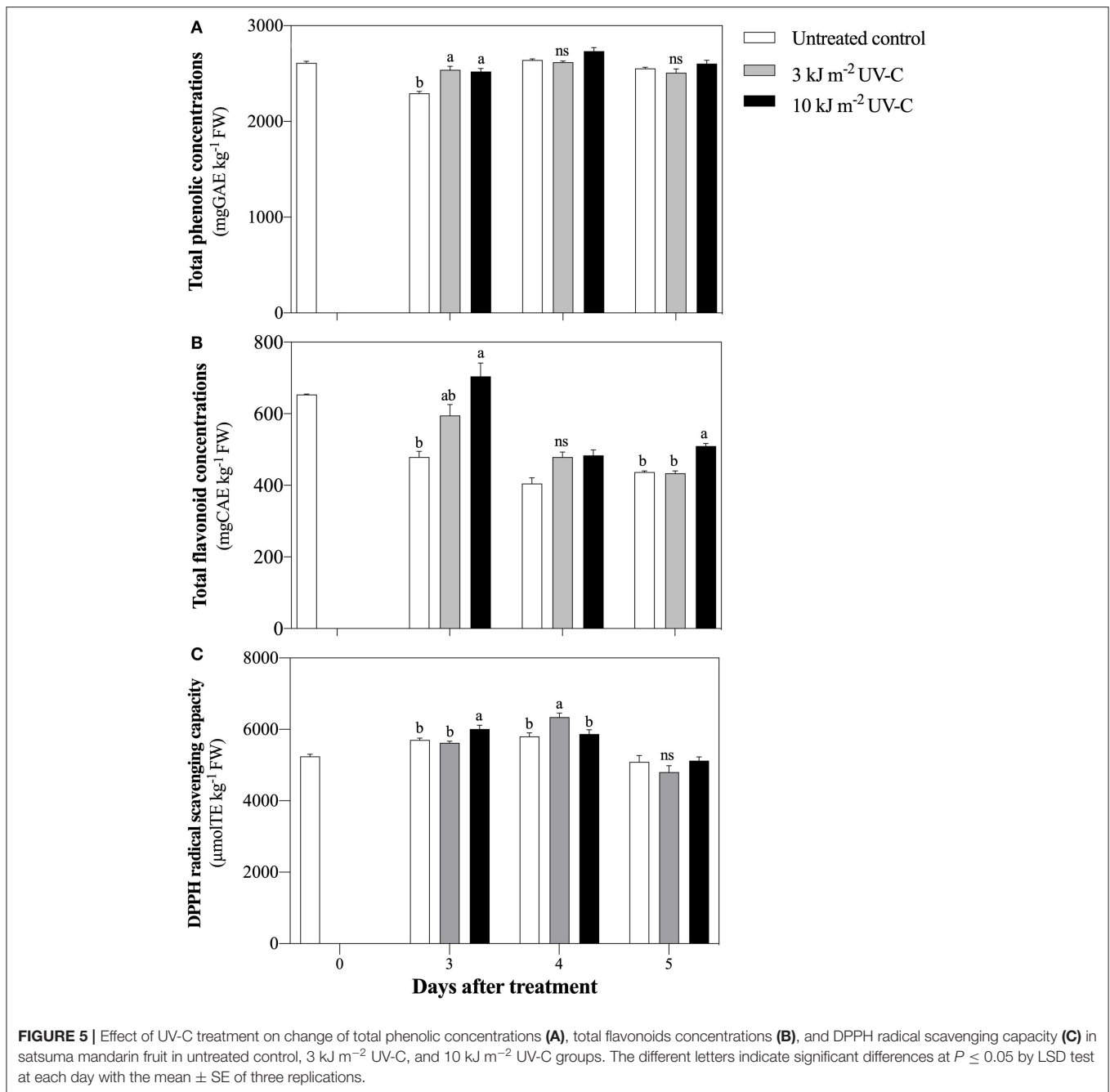


the other hand, MDA is the by-product of the lipid peroxidation process that occurs when reactive oxygen species (ROS) are exceeded in plant cells. This primary injury has been associated with withdrawal of electrons from membrane lipids, leading to membrane structure breakdown and high production of MDA (He et al., 2019). Pongprasert et al. (2011) confirmed that UV-C decreases MDA production in banana peel. In satsuma mandarin, 10 kJ m<sup>-2</sup> UV-C treatment reduced MDA concentrations after inoculation with *P. digitatum*. The significant decrease in lipid peroxidation formation was probably due to UV-C irradiation.

Pathogenic infection can be reduced by JA application in some crops such as sugar beet root (*Beta vulgaris*), grape (*Vitis vinifera*), and naranjilla (*Solanum quitoense*) (Fugate et al., 2012; Wang et al., 2015; Avila et al., 2019). Interestingly, Xu et al. (2016) demonstrated that UV-C application promoted the activation of JA signaling molecules

and biosynthetic pathway in *Arabidopsis thaliana*. In satsuma mandarin, an increase in endogenous JA concentrations was observed upon UV-C treatment of 10 kJ m<sup>-2</sup>. This suggests that the reduction of green mold infestation achieved in the UV-C treatments may be due to the accumulation of JA.

The total phenolic compounds act as the main precursor to stimulate antioxidant properties and increase disease resistance of various plants (Yoruk and Marshall, 2003). UV-C irradiation increases phenolic compounds by enhancing the activity of phenylalanine ammonia lyase (PAL), thereby participating in the phenolic biosynthetic pathway (Bhat et al., 2007). For example, Pataro et al. (2015) reported the increase in total phenolic concentrations in tomato fruit exposed to UV-C irradiation. However, in this study, UV-C treatments were found to increase the total phenolic concentration only on the



first day of the storage period. This result is in agreement with Sripong et al. (2019) who found that UV-C-irradiated mangosteen (*Garcinia mangostana*) fruit increased the defense against *Lasiodiplodia theobromae*, which corresponded with the induction of total phenolic accumulation. Both 3 and 10 kJ m<sup>-2</sup> UV-C irradiation also increased total flavonoid concentration compared to the untreated control. Shen et al. (2013) and Yang et al. (2019b) reported that UV-C treatment strongly promoted flavonoid concentration and therefore upregulated the expression levels of *flavonol synthase (FLS)*, *leucoanthocyanidin reductase (LAR)*, and *anthocyanidin reductase (ANR)* genes in

the flavonoid pathway in satsuma mandarin and blueberry (*Vaccinium corymbosum*) fruit.

All UV-C doses induced total antioxidant activity as measured by DPPH radical scavenging capacity in satsuma mandarin. As reported in previous studies, UV-C irradiation increased DPPH radical scavenging capacity in grape and papaya (*Carica papaya*) as well as total phenolic and flavonoid concentrations (Maurer et al., 2017; Sheng et al., 2018). Nevertheless, a decrease in total antioxidant activity in all treatments during the final storage period may be influenced by the depletion of total phenolic and flavonoid

concentrations. Our results showed that UV-C application activated total phenolic and total flavonoid concentrations and increased the ability to scavenge DPPH radicals; this promoted the plant defense mechanism against *P. digitatum* infection in satsuma mandarin fruit. From our study, promising UV-C irradiation with pathogen defense mechanism associated with bioactive compounds on fruit quality requires further studies.

## CONCLUSION

UV-C irradiation at a dose of 10 kJ m<sup>-2</sup> effectively maintained the integrity of the membrane structure by reducing lipid peroxidation and increasing JA accumulation with the induction of bioactive compounds and antioxidant potential of DPPH radical scavenging capacity. These results contributed to the inhibition of green mold infestation caused by *P. digitatum* in satsuma mandarin fruit. As shown in this study, UV-C irradiation has a very good potential to be considered as a safe alternative treatment for postharvest control of green mold diseases in citrus.

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## DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

## AUTHOR CONTRIBUTIONS

OP designed and conducted the experiment, analyzed the data, prepared the figures, and wrote the first draft of the manuscript. HO supported the material used in the experiment. MN critically reviewed and corrected the English. SK and SS conceived, supervised, and critically reviewed the manuscript. All authors contributed to the manuscript revision, read, and approved the submitted version.

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

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