Ultraviolet C (UV-C) irradiation is an excellent method for the induction of secondary metabolites in many plants. Thus far, various types of secondary metabolites have been induced by the application of different doses of UV-C irradiation either alone or in combination with other treatments. Especially, the treatment of a low dose of UV-C for up to 30 min allows the plants to partially recover to their normal physiological status and triggers the key enzymes of their metabolic pathway, ultimately leading to considerable increase in secondary metabolite. Increased levels of secondary metabolite vary from plant to plant. Apart from that, they also play crucial roles in UV protection. In this review, we will discuss various aspects of the accumulation of plant secondary metabolites by the irradiation of UV-C.

**Keywords:** Secondary metabolite, UV-C radiation, flavonoids, carotenoids.

Published online June 25, 2020
radiation in high dosage adversely affects growth and developmental processes in plants through a variety of methods: i) increasing the concentration of ROS and development of oxidative stress; ii) protein denaturation; iii) decreasing cell viability; and iv) causing cell death (Danon and Gallois, 1998; Zacchini and De Agazio, 2004; Procházková and Wilhelmová, 2007; Takeuchi et al., 2007; Nawkar et al., 2013). Further, prolonged UV-C exposure (more than 30 min) causes irreversible damage at both the physiological and morphological levels that leads to plant death. Low dosage of UV-C exposure (upto 30 min), however, allows plants to partially recover their normal physiological status and triggers adaptive responses in plants such as stimulate the enzymatic and non-enzymatic defense machinery (Katerova et al., 2009; Rai et al., 2011; Castronuovo et al., 2014).

Plant secondary metabolites (PSMs) are the unique source of color, taste, and fragrance. Further, they provide the plant's resistance against biotic and abiotic stresses, and hence, play a vital role in the plant defense system (Tiwari and Rana, 2015). Large numbers of PSMs have identified and classified into three major groups based on their metabolite biosynthetic pathways, i.e., terpenes, alkaloids, and phenolic compounds (Young, 1982; Ircihaiya et al., 2015). Some important PSMs such as flavonoids, stilbenes, and isoflavonoids have already revealed significant therapeutic effects on cancers and cardiovascular diseases as well as anti-aging agents (Baur and Sinclair, 2006; Goetzl et al., 2007; Perabo et al., 2008; Ma et al., 2013). Because of these functions, PSMs have been used in ancient traditional medicines and are also used in several industries such as cosmetics, fine chemicals, and more recently in nutritional products (Bourgaud et al., 2001).

Irradiation of UV-C can be used for accumulating PSMs without affecting their properties (Hasan and Bae, 2017), increasing the postharvest preservation of fruits and vegetables (Cao et al., 2010; Chen et al., 2016), and enhancing the food quality (Sripong et al., 2019; Wang et al., 2019) Thus, the use of UV-C has been recently shifted toward the potential to improve food quality beyond its principal role of sterilization. Therefore, in this review, we summarize the previous findings on PSM accumulation by UV-C and other chemical pretreatment combinations for enhancing valuable PSMs.

**UV-C induced biosynthesis of polyphenols**

**Total phenolics:** Phenolic compounds represent a huge class of PSMs, have diverse structures containing one or more hydroxyl groups and produced by plants mainly for protection against stress. UV-C irradiation increases the accumulation of phenolic compounds along with antioxidant properties. Induction of phenolic compounds was observed in lettuce plants (*Lactuca sativa* L.); however, it severely inhibited the growth of the plant (Lee et al., 2014). When compared with the control seedlings, UV-C treated broad bean showed significant increases in total phenolic compounds as well as in anthocyanin content throughout the germination period (Youonis et al., 2010). The total phenolic content (1.55 mg/100g) detected after 5 min UV-C exposure from 30 cm distance and incubation period of 24 h in the calli of Okuzgozu grape cultivar (Cetin, 2014). A higher amount of ANS and antioxidant capacity (AOX) was detected after UV-C treatment and thermovinification than classical maceration processes in the Bogazkere grape cultivar. Therefore, this technique can be utilized for phenolic- and antioxidant-rich red grapes in the winemaking industry (Tahmaz and Söylemezoğlu, 2017). Correspondingly, content of phenolic compounds also found to increase in UV-C treated (3.6 kJ/m²) table grape compared with untreated. Treatment leads to higher gene transcript level of PAL, CHS, STS and ANS, which are directly responsible for increase phenolic compounds (Sheng et al., 2018).

A recent study showed the combined effect of UV-C radiation and wounding intensity on phenolic compounds and AOX in carrot. The phenolic compounds (chlorogenic acid, ferulic acid, and isocoumarin) and AOX increased after UV-C radiation in cut carrots, whereas uncult carrots showed no effects (Surjadinata et al., 2017). Similarly, UV-C treatment also induces total phenolic content in potato slices and garden cress (*Lepidium sativum* L) calli during different storage periods, respectively (Teoh et al., 2016; Ullah et al., 2019).

**Flavonoids:** Flavonoids are secondary metabolites produced by plants that generally increase as a response to biotic or abiotic stress (Crupi et al., 2013). The maximum amount of total flavonol content was obtained without incubation after 5 min UV-C irradiation from 20 cm distance in the calli of Okuzgozu cultivar of grape. However, 24 h and 48 h incubation time are also suitable for total flavonol content after 5 min UV-C irradiation from 30 cm distance (Cetin, 2014). Studies also reported that UV-C treatment increased the total amount of flavonols and anthocyanins in strawberries, blueberries (Wang et al., 2009; Li et al., 2014) and the savory plant (*Satureja hortensis* L.) (Rahimzadeh et al., 2011). In the epidermis of table grapes, UV-C irradiation enhances the accumulation of flavonols and anthocyanins such as malvidin 3-glucoside, peonidin 3-glucoside, petunidin 3-glucoside, cyanidin 3-glucoside and delphinidin 3-glucoside (Cantos et al., 2000; Crupi et al., 2013). The rise in flavonoid accumulation induced by UV-C irradiation is also accountable for enhanced antioxidant activities and radical scavenging properties in fruits and vegetables (Wang et al., 2009; Li et al., 2014; Rivera-Pastrana et al., 2014).
pigmented flavonoids. However, UV-C tolerance was lost when crossed with a *transparent testa 4* (*tt4*) plant (this gene encoding the first enzyme of the flavonoid biosynthesis have mutated), confirming that flavonoids produced in the *tt4* mutant could defend against UV-C. It is also suggested that NADPH-dependent thioredoxin reductases act as a negative regulator for flavonoid biosynthesis (Bashandy et al., 2009).

The amount of anthocyanins, rutin, flavonoids and UV-absorbing compounds significantly increased when foliar sprayed with salicylic acid (SA) (27 min per day, up to 14 days) on UV-C treated pepper (*Capsicum annuum* L.) plants, as the foliar spray of SA hindered the effects of UV on pepper plant (Mahdavian et al., 2008). In another study, the flavonoid content was increased by 26% after UV-C irradiation (1.48kJ/m²) in mature green ‘Maradol’ papaya fruit, due to increased catalase and superoxide dismutase enzymatic activity (Rivera-Pastrana et al., 2014).

**Stilbenes:** Stilbene compounds are secondary metabolites belonging to the non-flavonoid phytoalexins group that plays an important role in biotic or abiotic stress (Cantos et al., 2002; Crupi et al., 2013). Grapes (*Vitis vinifera*) are the main source of stilbenes in the human diet. UV-C radiation is a prevalent technique for promoting the biosynthesis of the stilbene resveratrol in grape berries as well as processed grape products, i.e., grape juice and wine (Hasan and Bae, 2017). Various types of polyphenol compounds accumulated in the grape that protect against pathogens and environmental stresses including UV-C radiation (Suzuki et al., 2015). Mature grape berries were strongly induced by UV-C irradiation and have a high level of resveratrol accumulation (Adrian et al., 2000; Versari et al., 2001; Takayanagi et al., 2004; Suzuki et al., 2015). The trans-resveratrol was 355 times higher (3.492 µg/g fresh weight) than that in controls after UV-C irradiation (Suzuki et al., 2015). The UV-C irradiated grape leaves were found to accumulated resveratrol content up to 750 µg/g (fresh weight) after 10–15 min exposure at a close (15 cm) distance (Douillet-Breuil et al., 1999; Adrian et al., 2000; Versari et al., 2001). Thirty-minute UV-C irradiation can induce a 2-fold increase in resveratrol after 10 days incubation in the refrigerator (0°C) (Cantos et al., 2000). Mulberry leaves also rapidly accumulated oxyresveratrol (a potent tyrosinase inhibitor) after 30 min UV-C irradiation (Li et al., 2016).

The optimization of UV-C irradiation regarding the increased accumulation of resveratrol (10.8-fold higher relative to the untreated grape) in the fruit of table grape has been patented. The condition for treatment is as follows; range of irradiation intensity between 30–510W for less than 1 min and 2–4 days incubation period (González-Barrio et al., 2005; Guerrero et al., 2010). UV-C (254 nm) treatment followed by storage in the dark at 25°C boosted accumulation of resveratrol by 7- and 8-fold after 1 and 6 days respectively, in *V.amurensis*’Tonghua-3’(Yin et al., 2016).

The stilbenoids (resveratrol and piceid) increased 10-fold with 30 min postharvest UV-C treatment in ‘Napoleon’ cultivar of grapes (Cantos et al., 2001). These results indicate that potentially health-promoting resveratrol can be increased in table grapes by using UV-C irradiation. Red wine grape varieties Cabernet Sauvignon, Carinena, Garnacha, Merlot, Syrah and Tempranillo are evaluated for stilbene induction capacity after post-harvest UV-C irradiation. After exposure to UV-C irradiation, all the grape varieties were found to have a highcontent of resveratrol, piceatannol, and viniferin; however, in the variety ‘Monastrell’, the only piceatannol was induced. Here, total stilbene induction ability of the grapes ranged from 2.4-fold (in ‘Merlot’) to 10.9-fold (in both ‘Cabernet Sauvignon’ and ‘Carinena’) relative tocontrol. The highest induction for resveratrol was 22.7-fold in ‘Cabernet Sauvignon’, 6.4-fold for piceatannol ‘Carinena’, 3.8-fold for piceid ‘Tempranillo’ and 8.4-fold for c-viniferin in both ‘Cabernet Sauvignon’ and Carinena’ comparing to the control (Cantos et al., 2003a). Three minutes of UV-C irradiation followed by 48 h incubation at 4°C increased the contents of cis- and trans- piceid (34 µg/g and 90 µg/g of skin, respectively) in ‘Redglobe’ variety of grapes sampled (Crupi et al., 2013).

The treatment of leaves of *V. Vinifera* with UV-C and stilbene biosynthesis is well documented (Gindro et al., 2012; Jeandet et al., 2013), with *V. vinifera* and *Cissus quadrangularis* (of the Vitaceae family) known to produce various stilbenoids (Rivière et al., 2012). White table grapes, var. ‘Superior’, were treated with UV-C light after harvest to increase the concentration of stilbenes (González-Barrio et al., 2005). In another study, induction of stilbene in grape juice was observed 35 higher times after UV-C treatment followed by 2h maceration at 45°C and extracted using 0.2% sodium metabisulfite (González-Barrio et al., 2009). UV-C irradiated grapes showed some browning on the surface of the fruit, with a lower content of chlorophyll b and increased pheophytins. These results suggest that the development of browning in ‘Superior’ white grapes after UV-C treatment may be primarily due to the reduction of chlorophyll content (González-Barrio et al., 2005). Similarly, two ozone (O₃) gas concentrations (3.88 and 1.67 g/h) are used as postharvest treatment in seedless white table grapes (var. Superior) for 1, 3, and 5 h and increase in stilbenoid biosynthesis (trans-resveratrol, piceatannol and viniferin) through storage condition of 95% relative humidity and temperature 22°C. After two days
of storage, the highest resveratrol concentration was detected (González-Barrio et al., 2006).

The wine made from UV-C irradiated grapes was increased approximately 1.5-fold and 2-fold in piceatannol and resveratrol, respectively, as compared to berries, two genes encoding for a pathogenesis-related protein, chitinase of class IV (CHI4D) were irradiated by UV-C for 15 min, and the level of stilbenes was observed during the incubation period. Within 3 days of UV-C irradiation, the content of resveratrol, piceid, ϵ-viniferin, and pterostilbene was observed and concentration of two major stilbenes (resveratrol and ϵ-viniferin) accumulated to a high level up to >100 µg/g of fresh weight (Douillet-Breuil et al., 1999).

The trans-resveratrol levels in the berries of mature grape (Vitis spp.) significantly increased in UV-C irradiated than non-treated samples after 12 h post-treatment and continued to increase steadily until 60 h post-treatment (56.76 µg/g fresh weight). The content of cis-resveratrol at each time point did not vary significantly in response to the UV-C treatment (Yin et al., 2016). The trans-resveratrol content (8.43 µg/g) was noticed in V. vinifera cultivar exposed to UV-C for 5 min from 30 cm distance and incubated for 24 h i.e., ~8 fold induction was observed than those of control calli (Cetin, 2014). UV-C irradiation also stimulated resveratrol biosynthesis (primarily as trans-resveratrol) in V. vinifera ‘Beihong’. Young berries at 55 days after anthesis are highly sensitive to UV-C irradiation, with the total resveratrol in the skin of the UV-C irradiated berry about 90 times higher than that of the control (Wang et al., 2015). In another grape (V. vinifera ‘Corvina’), UV-C rays greatly stimulated the mRNA of STS in unripe berries (Versari et al., 2001). In UV-C exposed berries, two genes encoding for a pathogenesis-related protein, chitinase of class IV (CHI4D) and thaumatin-like (TL3), were strongly expressed before veraison (Colas et al., 2012).

A significantly higher amount of resveratrol accumulated after 48 h of UV-C irradiation in cultivar Muscat Bailey A (1910 µg/g fresh weight) as compared to the other two varieties. The expression pattern of a few genes such as PAL, CHS and STS was correlated with the induction of resveratrol through UV-C (Takayanagi et al., 2004). The levels of STS gene were up-regulated in grape leaves; however, the distribution of resveratrol and STS in grape was organ and tissue-specific (Wang et al., 2010). Before veraison, the expression level of STS genes was maximum and it decreased prior to maturity (Wang et al., 2015). After treatment with UV-C, a total of 22 STS genes have exhibited a high level of expression and these gene expression is a key factor influencing the accumulation of resveratrol. PAL genes along with the genes of cinnamate 4-hydroxylase (C4H) and 4-coumaroyl CoA ligase (4CL) was also up-regulated in response to UV-C treatment while the down-regulation of the CHS gene was observed (Xi et al., 2014; Suzuki et al., 2015). This observation proved that the inverse relationship between CHS and STS during UV-C irradiation exposure. Hence, accumulation of resveratrol in grape berries associated with the expression of both gene (Yin et al., 2016).

UV-C induces biosynthesis of terpenes

Saponins: The saponin content and the accumulation patterns of leaf triterpene saponins were observed in response to stress in leaves of Quillaja brasiliensis. The high yield of saponins also detected, when this plant exposed to jasmonic acid, salicylic acid, ultrasound, and UV-C light. These accumulated terpenes may be part of a defense response against stress (de Costa et al., 2013). Further, several studies have been documented for UV-C elicitor in commercial mushrooms cultivar to enhance the ergosterol (vitamin D2) content (Mau et al., 1988; Taofiq et al., 2017).

Carotenoids: Savory (S. hortensis L.) plants are sensitive to UV-C and exhibited a significant reduction in carotenoid contents after 8 days of UV-C treatment (Rahimzadeh et al., 2011). Similarly, UV-C irradiation also increases the carotenoid compound, lycopene, two-fold in mature green tomatoes by application of different doses (Bravo et al., 2012). In recent study, the combined treatment of UV-C (2.15 kJ/m2) and ultrasonic energy have increased the lycopene content in tomato fruits by 90% than control (Esua et al., 2019).

The details of all types of PSMs induced by UV-C irradiation are summarized in Table 1. Most of the study used V. vinifera as source plant with a different time period of treatment.
### Table 1. Summary of plant secondary metabolites induced by UV-C irradiation

<table>
<thead>
<tr>
<th>PSMs</th>
<th>Source</th>
<th>Treatment Condition</th>
<th>UV-C elicitation dose</th>
<th>Induced by References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ergosterol</td>
<td><em>Agaricus bisporus</em></td>
<td>UV-C</td>
<td>14.71 kJ/m²</td>
<td>3.31 fold (Mau et al., 1998; Taofiq et al., 2017)</td>
</tr>
<tr>
<td>Resveratrol</td>
<td><em>Vitis vinifera</em> cv. Beihong</td>
<td>UV-C</td>
<td>6 J/m²</td>
<td>90 fold (Wang et al., 2015)</td>
</tr>
<tr>
<td>Total flavonoids</td>
<td><em>Vitis vinifera</em> cv. Okuzgozu calli</td>
<td>UV-C, stored at 0°C</td>
<td>25.2-57.6 kJ/cm²</td>
<td>8 fold (Cetin, 2014)</td>
</tr>
<tr>
<td>Flavonoids</td>
<td><em>Capsicum annuum</em> L.</td>
<td>UV-C+SA</td>
<td>5.7 J/m²</td>
<td>1.5-2 fold (Mahdavian et al., 2008)</td>
</tr>
<tr>
<td>Catechin</td>
<td><em>Vitis vinifera</em> cv. Redglobe</td>
<td>UV-C, stored at 4°C</td>
<td>4.1 kJ/m²</td>
<td>1.5 to 2 fold (Crupi et al., 2013)</td>
</tr>
<tr>
<td>Catechin</td>
<td><em>Vitis vinifera</em> cv. Okuzgozu calli</td>
<td>UV-C</td>
<td>50.4-115.2 kJ/cm²</td>
<td>7.28 fold (Cetin, 2014)</td>
</tr>
<tr>
<td>Cis and trans piceid</td>
<td><em>Vitis vinifera</em> cv. Redglobe</td>
<td>UV-C, 4°C</td>
<td>2.4 kJ/m²</td>
<td>3 fold (Crupi et al., 2013)</td>
</tr>
<tr>
<td>Piceid</td>
<td><em>Vitis vinifera</em> cv. Napoleon</td>
<td>UV-C, 0°C</td>
<td>17.8–23.0 J/m2</td>
<td>3 fold (Cantos et al., 2000)</td>
</tr>
<tr>
<td>Cyanin-3-O-glucoside, peonidin-3-O-glucoside</td>
<td><em>Vitis vinifera</em> cv. Redglobe</td>
<td>UV-C, 4°C</td>
<td>4.1 kJ/m²</td>
<td>1.5 to 2 fold (Crupi et al., 2013)</td>
</tr>
<tr>
<td>Carthamin</td>
<td><em>Carthamus tinctorius</em> L. cv. Benibana</td>
<td>UV-C, 23°C</td>
<td>50 J/m²</td>
<td>13.9 fold (Fukushima and Saito, 2000)</td>
</tr>
<tr>
<td>Anthocyanins</td>
<td><em>Capsicum annuum</em> L.</td>
<td>UV-C+SA</td>
<td>5.7 J/m²</td>
<td>2 fold (Mahdavian et al., 2008)</td>
</tr>
<tr>
<td>Rutin</td>
<td><em>Capsicum annuum</em> L.</td>
<td>UV-C+SA</td>
<td>5.7 J/m²</td>
<td>3 fold (Mahdavian et al., 2008)</td>
</tr>
<tr>
<td>UV absorbing compounds</td>
<td><em>Capsicum annuum</em> L.</td>
<td>UV-C+SA</td>
<td>5.7 J/m²</td>
<td>2 fold (Mahdavian et al., 2008)</td>
</tr>
<tr>
<td>Artemisinin</td>
<td><em>Artemisia annua</em> L.</td>
<td>UV-C</td>
<td>5.7 kJ/m²</td>
<td>15.7% (Rai et al., 2011)</td>
</tr>
<tr>
<td>Lycopene</td>
<td><em>Lycopersicon esculentum</em> L.</td>
<td>UV-C, stored at 25°C</td>
<td>3.0 kJ/m²</td>
<td>2 fold (Bravo et al., 2012)</td>
</tr>
<tr>
<td>Lycopene</td>
<td><em>Lycopersicon esculentum</em> L.</td>
<td>UV-C and ultrasound</td>
<td>2.15 kJ/m²</td>
<td>90% (Esua et al., 2019)</td>
</tr>
<tr>
<td>Glucosinolate</td>
<td><em>Brassica oleracea</em> L. cv. italica</td>
<td>UV-C, stored at 4°C</td>
<td>1.2 kJ/m²</td>
<td>N/A (Nadeau et al., 2012)</td>
</tr>
<tr>
<td>Lignans (Di-glucoside)</td>
<td><em>Linum usitatissimum</em> L.</td>
<td>UV-C</td>
<td>3.6 kJ/m²</td>
<td>1.86 to 2.25 fold (Anjum et al., 2017)</td>
</tr>
<tr>
<td>Total phenolic</td>
<td><em>Linum usitatissimum</em> L.</td>
<td>UV-C</td>
<td>3.6 kJ/m²</td>
<td>2.82 fold (Anjum et al., 2017)</td>
</tr>
<tr>
<td>Polyphenols</td>
<td><em>Lepidium sativum</em> L.</td>
<td>UV-C</td>
<td>3 J/m²</td>
<td>2.5 fold (Ullah et al., 2019)</td>
</tr>
</tbody>
</table>
Conclusions and future prospects: To conclude, UV-C radiation impairs primary metabolism of plants and has shown substantial promotion of the accumulation of secondary metabolites. UV radiation generates a hypothetical ROS-mediated mechanism and has the potential to damage macromolecules such as, DNA, protein and, also target their photosynthetic system. In many scenarios, UV-C irradiation has been directly correlated with the regulation of key biosynthetic enzymes such as PAL, CHS, STS, and ANS. Low dose UV-C irradiation could act as elicitors for these secondary metabolic enzymes under controlled conditions in plants and these accumulated secondary metabolites also protect against UV-damage. To attain the efficient production, we need to determine the optimum dose by illuminating wide range of irradiation intensity and exposure time. Additionally, the accumulation of these secondary metabolites could also influence by other combining elicitors. Considerably, many researches are figure out the molecular basis of UV-C hormesis and their metabolic response in recent years. However, the exact signaling mechanism of UV-C elicitation are still unknown and require additional experimental studies to elucidate the mechanism.

Acknowledgments: This study was supported by the Basic Science Research Program through the National Research Foundation of Korea (NRF) funded by the Ministry of Education (NRF-2019R1F1A1052625).

Author Contributions: KHB conceived and designed the study. AKM, SC and KHB contributed to the writing of the manuscript.

Conflicts of Interest: The authors declare no conflict of interest.

REFERENCES


