ITU Journal of Food Science and Technology

ITU/JFST

Effects of Ultraviolet – C Treatment on Postharvest Physiologies and Decay of Berries: A Review

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Abstract: Berries have a short shelf-life due to their high metabolic activities and susceptibility to weight loss, mechanical damage, softening, and microbial decay. Ultraviolet-C light (UVC) treatment, a non-thermal and non-chemical method, has improved the microbiological, physiological, and nutritional quality of postharvest fruit and vegetables. This review examines postharvest berry physiology such as ethylene production, respiration rate, texture (firmness, weight loss, and cell wall), phenolic compounds, antioxidant capacity, color, flavor, and microbial decay during storage as affected by UVC treatment. Studies have shown that UVC treatment has a beneficial effect on increasing phenolic compounds, antioxidant capacity, and maintaining the firmness of berries. Besides, softening and weight loss can be inhibited in UVC-treated berries during postharvest. However, UVC treatment can increase ethylene production and respiration rate, causing flavor degradation and early senescence. The effectiveness of UVC treatment depends on berry cultivars, UVC doses, and other processing parameters. Moreover, combining physical and chemical treatments with UVC in a hurdle approach may enhance berry physiology compared to UVC treatment alone.

Keywords: Berry, UVC, respiration, ethylene, texture, bioactive compounds.

Ultraviyole-C Uygulamasının Hasat Sonrası Dutsu Meyvelerin Fizyolojisine ve Bozulmasına Etkisi: Derleme

Özet: Dutsu meyveler yüksek metabolik aktivite, ağırlık kaybı, yumuşama ve mikrobiyal çürümeye yatkınlıkları nedeniyle kısa raf ömrüne sahiptir. Isıl ve kimyasal olmayan bir yöntem olan ultraviyole-C ışık (UVC) uygulaması, hasat sonrası meyve ve sebzelerin mikrobiyolojik, fizyolojik ve besinsel kalitesini iyileştirmek için kullanılmaktadır. Bu derlemede, hasat sonrası UVC uygulamasının dutsu meyvelerde etilen üretimi, solunum hızı, doku (sertlik, ağırlık kaybı ve hücre duvarı), fenolik bileşikler, antioksidan kapasite, renk, lezzet ve mikrobiyal çürüme gibi kalite özellikleri üzerine etkileri incelenmiştir. Çalışmalar, UVC uygulamasının dutsu meyvelerde fenolik bileşikleri ve antioksidan kapasiteyi arttırmada ve meyvelerin sertliğini korumada yararlı bir etkiye sahip olduğunu göstermiştir. Ayrıca, hasat sonrasında UVC ile muamele edilen meyvelerde yumuşama ve ağırlık kaybı engellenebilmektedir. Bununla birlikte, UVC uygulaması etilen üretimini ve solunum hızını artırarak aromanın bozulmasına ve erken yaşlanmaya neden olabilmektedir. UVC uygulamasının etkinliği meyve çeşitlerine, UVC dozuna ve diğer uygulama parametrelerine bağlıdır. Ayrıca, engel teknolojisi kullanılarak fiziksel ve kimyasal uygulamaların UVC ile kombinasyonu, tek başına UVC işlemine kıyasla dutsu meyvelerin fizyolojisinde daha olumlu etkilere neden olabilir.

Anahtar Kelimeler: Dutsu meyveler, UVC, solunum, etilen, tekstür, biyoaktif bileşikler.

Review

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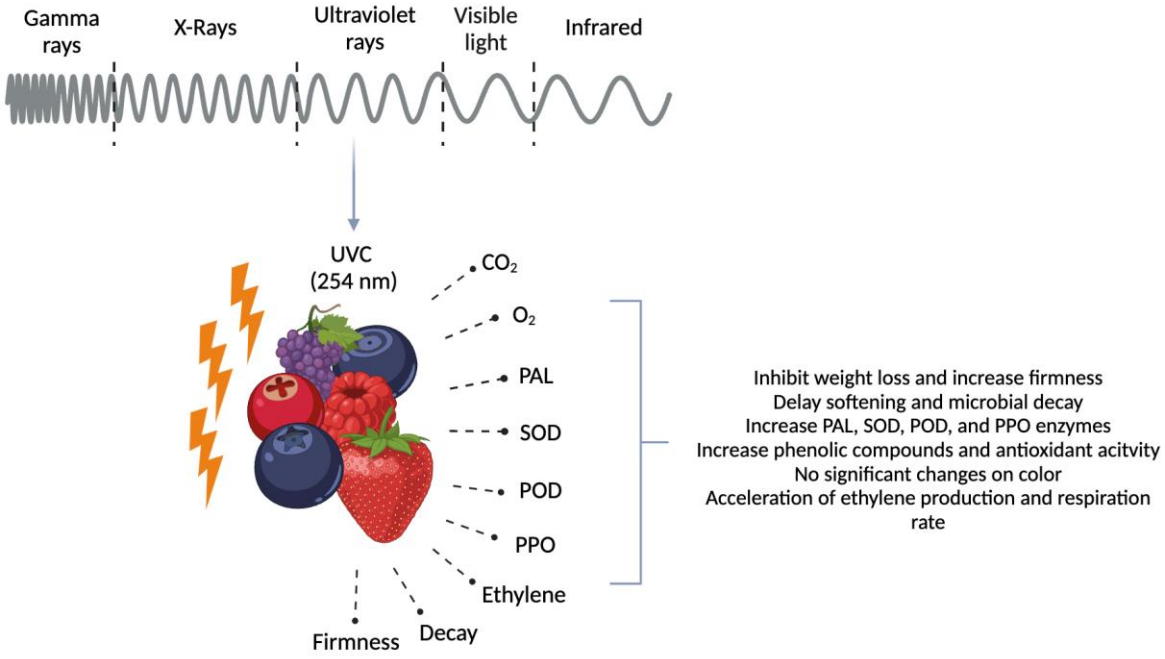
Reference: Bilgin, A. B. & Gunes, G. (2024). Effects of ultraviolet – C treatment on postharvest physiologies and decay of berries: A review, *ITU Journal of Food Science and Technology*, *2*(2), 85-100.

Submission Date: 1 July 2024
Online Acceptance: 18 August 2024
Online Publishing: 30 September 2024

Graphical Abstract



1. Introduction

Berries are small, soft-fleshed fruits that ripen from the ovary wall's outer layer into an edible pericarp (Dickenson, 2020). Berries, including blueberries, cranberries, blackberries, raspberries, strawberries, black currant, chokeberry, mulberry, and acai, are commonly used in culinary customs due to their visual appearance and high secondary metabolite content such as flavonoids (anthocyanins, flavanols, and flavonols), phenolic acids, tannins, ascorbic acid, and carotenoids (Horvitz, 2017; Skrovankova et al., 2015; Szajdek & Borowska, 2008). In addition to being high in fiber, natural vitamins and antioxidants are contained in berries (Basu et al., 2010). They are beneficial for human health due to their antioxidant and anti-inflammatory properties, which can lower the risk of cancer, cardiovascular disease, diabetes, and cataracts (Padmanabhan et al., 2016; Vidovic, 2018). Additionally, consuming berries can delay cognitive aging (Devore et al., 2012).

Berries are highly perishable and have short storage life due to their high metabolic activities and susceptibilities to pathogen attack, mechanical damage, and moisture loss (Liu et al., 2019; Van der Steen et al., 2002). To ensure high quality and extended shelf life, it is crucial to harvest and handle berries at optimum ripening stages with precise methods (Baietto & Wilson, 2015). After harvesting, berries' quality and nutritional value decrease readily due to mechanical damage, improper handling, and being highly perishable and susceptible to spoilage (Liu et al., 2019; Skrovankova et al., 2015). They are consumed as fresh, frozen, or processed into pulp, purees, jams, jellies, and juices (EFSA, 2014; Pritts, 2017). Nevertheless, a significant fraction of them become waste after postharvest processing (Kaur et al., 2022). The commercial preservation of the whole berries is carried out using non-destructive and non-thermal methods such as cold storage (Liu et al., 2019). Alternatively, controlled atmosphere storage (Gunes et al., 2002), modified atmosphere packaging (Gimeno et al., 2021), gamma-irradiation (Basaran and Kepenek, 2011; C. Wang et al., 2017), ozone (Piechowiak, 2021; Piechowiak et al., 2021), edible coating (Ascencio-Arteaga et al., 2022; Falcó et al., 2019), high-pressure processing (Lou et al., 2022), cold plasma (Ji et al., 2020; Lacombe et al., 2015), and their combination (Pinto et al., 2020; Rodriguez and Zoffoli, 2016) have been searched to prolong berries' shelf-life, inhibit microbial decay, and ensure food safety against microorganisms such as *Salmonella, Botrytis cinerea* and norovirus.

In recent decades, ultraviolet-C (UVC) light has been used as a non-thermal and non-chemical technique to ensure the quality and safety of postharvest berries. Numerous research studies have extensively examined the postharvest physiology of UVC-treated berries, such as strawberries (Jin et al., 2017; Li et al., 2019), blueberries (Jaramillo Sánchez et al., 2021), raspberries (Gimeno et al., 2021). Nevertheless, there is no recent review on UVC effects on the post-harvest physiology of berries. Therefore, this study aims to discuss the effects of UVC treatments on various physiological aspects such as respiration rate, ethylene biosynthesis, texture (including cell wall degradation, firmness, and weight loss), phenolic compounds (flavonoids, non-flavonoids), antioxidant capacity, flavor, texture, color, and microbial decay in berries such as strawberry (*Fragaria ananassa*), raspberry (*Rubus idaeus*), blueberry (*Vaccinium* spp.), and boysenberry (*Rubus ursinus* × *Rubus idaeus*) during postharvest storage. The effects of combined treatments with UVC are also discussed.

2. Ultraviolet-C treatments: principles and application parameters

Ultraviolet (UV) region (100 – 400 nm) is placed between X-ray and visible light in the electromagnetic spectrum (Lewis, 2023). UVC refers to 200 – 280 nm and has germicidal effects on microorganisms, especially at 254 nm. Sun is a natural source of UVC light, but the ozone layer in the atmosphere absorbs it so that the Earth is protected from its harmful effects (Koutchma, 2019; Urban et al., 2016). Artificial UVC sources used in research and industry have included low- and medium-pressure mercury lamps and xenon lamps. Mercury-based lighting is widely used due to its prevalence in the market and the FDA's approval of low-pressure (LP) mercury lamps (253.7 nm) (Darré et al., 2022; FDA, 2013). FDA has

approved the use of xenon lamps and LP mercury lamps emitting a 253.7 nm wavelength for reducing pathogens and microorganisms on juice products, sterilizing potable water used in food production, and controlling surface microorganisms on food and food products in food processing and treatments under regulation 21CFR179.39 since 2000. However, as LP mercury lamps contain toxic mercury, the transition to mercury-free lighting is planned with the Minimata Convention on Mercury for Climate Action (Minamata Convention on Mercury, 2023). As an alternative, light-emitting diodes (LEDs) are suggested being mercury-free. LEDs have also been utilized due to their compactness, small size, low cost, and non-fragile structure during the last couple of decades (Cassar et al., 2020).

UVC light can be absorbed, reflected, or scattered on materials or food matrices. The UVC treatment dose expressed as kJ/m^2, is related to intensity and exposure time (Koutchma, 2014). UVC treatment effectiveness may be reduced due to its absorption by soluble materials and suspended particles in the food matrix and it may not reach all parts of the food matrix (Delorme et al., 2020). Therefore, it cannot penetrate turbid liquid and solid food although it can easily penetrate through pure water (Choudhary and Bandla, 2012; Koutchma, 2008). Thus, UVC treatment is generally considered as a surface treatment. Various studies have been conducted to examine inactivation effects of UVC light on surface microorganisms in foods including fruits and vegetables such as lettuce, strawberries, and tomatoes (Cho et al., 2022), cherries (Kutlu et al., 2022), fresh-cut pitaya (Zhai et al., 2021), strawberries (Janisiewicz et al., 2021; Ortiz-Solà et al., 2021), apple (Rios de Souza et al., 2020), lettuce (Green et al., 2020), oranges (Gündüz et al., 2015), pear (Sun et al., 2022), apricot (Hakguder Taze and Unluturk, 2018). Dose, exposure times, wavelength, light sources, the distance of sample and lamps, the number of UVC lamps and their position, uniform distribution of light on all surfaces (effective exposure), temperature, type and characteristics of foods, type of microorganism on food surfaces, are vital parameters to determine the efficiency of the UVC treatment. UVC can inhibit DNA replication and transcription by forming DNA photoproducts like pyrimidine 6-4 pyrimidone and cyclobutene pyrimidine dimers, leading to mutagenesis and cell death (Artés and Allende, 2015; Harm, 1980).

3. Effects of UVC on Postharvest Berries Physiology

Postharvest storage of fruit and vegetables is accompanied by cellular respiration which involves the breakdown of macromolecules (i.e., carbohydrates, lipids, etc.) to produce ATP/energy through glycolysis, tricarboxylic acid cycle (TCA) cycle, and electron transport chain. Respiration rate is affected by the physiological conditions of the fresh produce and storage atmosphere conditions such as temperature, relative humidity, and modified atmospheres (MA). Most berries are non-climacteric fruits; they do not ripen after harvesting. So, they must be harvested at horticultural maturity. Their quality and nutritional content can be significantly reduced during storage (Liu et al., 2019). They are highly perishable and susceptible to weight loss, softening, microbial spoilage, and decaying (Horvitz, 2017; Paniagua et al., 2013). Moreover, their postharvest shelf-life barely exceeds 2 – 6 weeks under typical refrigeration conditions during storage (Gimeno et al., 2021; Khanizadeh et al., 2009; Xu and Liu, 2017).

3.1. Ethylene biosynthesis and respiration rate

Ethylene biosynthesis

Ethylene, a natural plant hormone, plays a vital role in the ripening of fruits. Berries are mainly non-climacteric fruits. However, blackberries can be both climacteric (Walsh et al., 1983) and non-climacteric (Lipe, 1978), depending on their cultivars. Similarly, blueberries also vary in ethylene production depending on their cultivars (Farneti et al., 2022). However, ethylene production is mainly low in berries such as cranberry, blackberry, and raspberry, with production rates ranging from < 0.10, 0.32 – 0.40, and 0.29 – 0.49 µL/kg.h, irrespective of cultivars during postharvest storage (Gunes et al., 2002; Shah et al., 2023). Furthermore, strawberries, blackcurrants, mulberries, acai, bilberries, and gooseberries have relatively low ethylene production and respiration rates after harvesting (Fan et al., 2022). Only a few studies have established the effects of postharvest UVC treatment on ethylene production in berries (Table 1). For instance, Xu and Liu (2017) showed that although blueberries' ethylene production increased during 8-d storage at 4 °C, untreated and UVC-treated samples showed no significant difference in ethylene production (3.2 – 3.4 µL/kg.h). In contrast, Li et al. (2014) found that UVC treatment increased ethylene production of strawberries initially, and its level remained 4.4 and 11.7 times higher than that in untreated fruits after 1 and 4 d, respectively. Similarly, 4 kJ/m^2 UVC treatment increased ethylene production in strawberries in the first 6 h (Nigro et al., 2000). The increase in ethylene might be induced due to the activation of strawberry defense system against stress (Li et al., 2014; Nigro et al., 2000). However, ethylene production decreased in treated strawberries at the end of the storage (48 h) (Li et al., 2014; Nigro et al., 2000). However, the decrease of samples at the end of the 48 h was higher than the control (Nigro et al., 2000). Therefore, UVC can stimulate ethylene production immediately after the treatment, but it can be decreased substantially at the end of the storage in some berries.

Respiration rate

During the postharvest term, berries have mainly high respiration rates (41 – 245 mg CO_2/kg.h at 20 °C) (Huynh et al., 2019). For instance, ripe blackberry and raspberry have 41.4 – 53.28 and 45 – 76.32 mg CO_2/kg.h respiration rate at 20 °C, respectively (Shah et al., 2023). Transpiration and respiration are the primary causes of nutrient and water loss during storage, leading to weight loss in postharvest berries. The higher the respiration rate the higher the metabolic activity leading to shorter storage life (Bovi et al., 2019). Contrasting findings have been reported on UVC treatment effects on berries' respiration rate (Table 1). Postharvest blueberries' respiration rate increased by UVC treatment at 4 kJ/m^2 during 8-d of storage at 4 °C (Xu et al., 2016; Xu & Liu, 2017). UVC treatment at 4 kJ/m^2 suppressed the respiration rate to ~2.1 mg CO_2/kg compared to the untreated samples (2.43 mg CO_2 kg.h) at 4 °C in blueberries (Xu et al., 2016). Similarly, red raspberries' respiration rates were slightly increased from 10.03 to 14.67 mL CO_2/kg.h by UVC treatments at 2 and 4 kJ/m^2 during 12 d storage at 6°C (Gimeno et al., 2021). UVC treatment (1 - 15 kJ/m^2 dose) did not affect the respiration rate of strawberries at the end of the 6-d storage at 2°C (Allende et al., 2007). However, another study showed that the UVC treatment at 4 kJ/m^2 decreased the respiration rate of strawberries after 5 d of storage (Cote et al., 2013). Similarly, UVC treatment at 9.2 kJ/m^2 inhibited the respiration rate of boysenberry by 24.22 % and 7.92 % during storage for 1 d at 20 °C and 4 d at 4 °C, respectively (Vicente et al., 2004). The inhibitory effects of UVC treatment on the respiration rate of berries might be due to delaying microbial decay and cell wall degradation, as discussed in other sections in this review. The impact of the treatment depends on the applied dose, temperature, type, and physiological conditions of the berries. Few studies have been conducted on UVC treatment effects on berries' respiration rate (Table 1). Therefore, further research is required to get more precise results.

Table 1. Effect of postharvest ultraviolet-C treatment on berries' ethylene biosynthesis and respiration rate.
Tablo 1. Hasat sonrası ultraviyole-C uygulamasının dutsu meyvelerin etilen biyosentezi ve solunum oranı üzerindeki etkisi.

Berries	Dose (kJ/m^2)	Ethylene biosynthesis (µL/kg.h)	Respiration rate (CO_2 /kg.h)	References
Blueberry (*Vaccinium* spp. Berkeley)	4	NA	Decreased from 2.43 to ~2.1 mg	(Xu et al., 2016)
Blueberry (*Vaccinium* spp. Berkeley)	4	Unaffected (3.2 – 3.4)	Increased from 2.43 to > 2.5 mg	(Xu and Liu, 2017)
Boysenberry	9.2	NA	Decreased from 116.92 to 107.65 mL	(Vicente et al., 2004)
Red raspberry (*Rubus idaeus* L.)	2 and 4	NA	Increased from 10.03 ± 1.02 to 14.67 ± 1.60 mL	(Gimeno et al., 2021)
Strawberries (*Fragaria* × *ananassa* Duch., cv. *Camarosa*)	4	NA	Decreased	(Cote et al., 2013)
Strawberry (*Fragaria ananassa* Duch. cv. Akihime)	4.1	Increased 4.4 and 11.7-fold on 1 and 4 d, respectively	NA	(Li et al., 2014)

NA: not assessed

3.2. Texture (firmness, weight loss, and cell wall)

Maintenance of textural quality of berries is crucial for consumer acceptance and shelf-life. Key parameters for textural evaluation include firmness, weight loss, and cell wall enzymes and components in berries as reported by various researchers (Table 2).

Firmness

Firmness of berries decreases at refrigerated and room temperature during postharvest storage. Most studies have demonstrated that UVC treatment significantly prevented the loss of firmness in berries. For instance, Amiri et al. (2021) reported that UVC treatment at 0.5 kJ/m^2 resulted in higher firmness (2.47 N) in strawberries compared to the control samples (2.15 N) after 12 d storage at 5 °C. Also, UVC treatment with 4 kJ/m^2 doses ranging from single to multi-step increased strawberry hardness and compression resistance after 13 d of storage at 0 °C (Ortiz Araque et al., 2019). Similarly, UVC treatment at 6 kJ/m^2 resulted in better retention of firmness in blueberry compared to control samples after 28-d storage at 0°C (Nguyen et al., 2014). Nevertheless, Perkins-Veazie et al. (2008) reported that blueberries' firmness remained unaffected by treatments at 1 – 4 kJ/m^2 doses. Jaramillo Sánchez et al. (2021) evaluated the epicarp and mesocarp of blueberries post-UVC treatment and found that the treatment did not significantly impact the rupture force and deformation. Gimeno et al. (2021) found that UVC treatment at 4 kJ/m^2 caused a 12.5 % reduction in the firmness of red raspberry compared to the control while treatment at a lower dose (2 kJ/m^2) resulted in a 7.5 % increase in the firmness compared to the control after 12 d storage at 6 °C. Overall, several studies have shown that UVC treatment maintained the flesh firmness of berries such as strawberries (Amiri et al., 2021; Li et al., 2014; Severo et al., 2015), blueberries (Jaramillo Sánchez et al., 2021; Nguyen et al., 2014; Perkins-Veazie et al., 2008; Xu et al., 2016), and red raspberries (Gimeno et al., 2021), as shown in Table 2.

Weight loss

Water vapor released during transpiration and respiration causes weight loss in berries due to increased membrane permeability and decreased cell strength (Lu et al., 2016; Xu et al., 2016). In addition to inhibiting loss of firmness, UVC treatment can reduce weight loss. Several studies demonstrated that UVC treatment decreased the accelerated weight loss in berries such as blueberry (Nguyen et al., 2014; Xu et al., 2016), red raspberry (Gimeno et al., 2021), and strawberry (Amiri et al., 2021), as shown in Table 2. For instance, the weight loss of strawberries exposed to UVC at 0.5 kJ/m^2 was 1 %, while the control group was 1.95 % after 12 d of storage at 5 °C and 90 % relative humidity (Amiri et al., 2021). Besides, the weight loss of UVC-treated blueberries declined by ~1.3 % compared to untreated ones after 21 d of storage (Nguyen et al., 2014). Moreover, the weight loss of UVC-treated blueberries (~1.8 %) was lower than that of the control samples (2.6 %) after 8-d of storage at 4 °C (Xu et al., 2016). However, other studies reported no effect of UVC treatment on the weight loss of blueberries (Jaramillo Sánchez et al., 2021; Perkins-Veazie et al., 2008). The mechanism of UVC treatment for the reduction of weight loss is unclear. Reduced respiration rate may be associated with reduced weight loss. (Xu et al., 2016) showed that respiration rate and weight loss had a strong correlation (R = 0.869). Besides, UVC treatment may minimize weight loss by forming a thin dry layer on the surface of the commodity, which may inhibit the release of water vapor (Abdipour et al., 2020).

Cell wall metabolism

Cell walls in fruit and vegetables, particularly berries with thinner-skinned fruit, affect their textural quality and softening. Changes in the primary cell wall constituents such as cellulose (CEL), hemicelluloses (HCEL), and water-soluble pectin (WSP), the strength of adhesion in middle lamella, and the cell turgor can be associated with the loss of firmness and flavor (Chen et al., 2015). Besides, enzyme activities, such as cellulase (CL), polygalacturonases (PG), pectin methylesterase (PME), pectin lyase (PL), and rhamnogalacturonan lyase (RGL), can also cause deformation of cell wall structure and softening (Pombo et al., 2009; Priya Sethu et al., 1996; Sheng et al., 2018). Moreover, β-glycanases and β-glucosidases (β-gal) cleave xyloglucan, a common HCEL polymer (Ortiz Araque et al., 2019), while β-galactosidase promotes flesh softening by eliminating galactose from cell wall components (Trainotti et al., 2001).

Ortiz Araque et al. (2019) reported that UVC treatment inhibited the activity of β-glucanase, PG, PME, β-gal, and Xylase in strawberries after 13-d storage at 0 °C in darkness and preserved firmness. Severo et al. (2015) found that UVC treatment of strawberries may enhance firmness, inhibit cell wall degradation, and delay surface deterioration due to decreasing PL transcription genes despite increasing β-gal, PG, and PME genes compared to the control. Besides, Pombo et al. (2009) found that PG, PME, and endoglucanase were decreased or unaffected in strawberries by UVC treatment compared to control. In addition, they concluded that UVC treatment at 4.1 kJ/m^2 delayed strawberry softening, possibly due to decreased gene transcription involved in cell wall degradation (Pombo et al., 2009). Thus, UVC treatment can delay softening and maintain strawberry texture by reducing weight loss, pectin solubilization, and inhibiting cell

wall degrading enzyme activity. The evaluations on the effects of UVC treatment on strawberries' cell wall metabolism were reported (Ortiz Araque et al., 2019; Pombo et al., 2009; Severo et al., 2015) but, further research on other berries is needed.

Table 2. Effect of postharvest ultraviolet-C treatment on berries' texture (firmness, weight loss, and cell wall).
Tablo 2. Hasat sonrası ultraviyole-C uygulamasının dutsu meyvelerin tekstür (sıkılık, ağırlık kaybı ve hücre duvarı) üzerindeki etkisi.

Berries	Dose (kJ/m^2)	Firmness	Weight loss (%)	Cell wall	References
Blueberry	1 – 4	Unaffected	Unaffected	NA	(Perkins-Veazie et al., 2008)
Blueberry	<11.4	NA	Unaffected	NA	(Jaramillo Sánchez et al., 2021)
Blueberry	4	Inhibited loss of firmness	Decreased from 2.6 to ~1.8	NA	(Xu et al., 2016)
Blueberry	6	Increased ~0.3 N	Decreased by ~1.3	NA	(Nguyen et al., 2014)
Red raspberry	2 and 4	Increased by 7.5 % at 2 kJ/m^2 but decreased by 12.5 % at 4 kJ/m^2	Decreased from 8.1 to 6.9	NA	(Gimeno et al., 2021)
Strawberry	4.1	Increased from ~2.9 to ~3.2 N	NA	Decreased or unaffected PG, endoglucanases, and PME	(Pombo et al., 2009)
Strawberry	4.35	Increased by ~0.5 N	NA	Decreased pectate lyases transcript accumulation	(Severo et al., 2015)
Strawberry	4.1	Increased	NA	NA	(Li et al., 2014)
Strawberry	0.5	Increased from 2.47 to 2.15 N	Decreased from 1.95 to 1	NA	(Amiri et al., 2021)
Strawberry	Single-Step: 4 Two-Step: 2 x 2 Multi-Step: 5 x 0.8	Increased	NA	Decreased β-glucanase, PG, and PME activity and WSP	(Ortiz Araque et al., 2019)

NA: not assessed, ND: not determined, PG: polygalacturonases, PME: pectin methyl esterase, WSP: water-soluble pectin

3.3. Phenolic compounds

Berries contain phenolic compounds, including phenolic acids, flavonoids, and tannins, which contribute to their color and antioxidant capacity (Horvitz, 2017; Szajdek & Borowska, 2008). These compounds are formed in the epidermis and tissue and can be found in water-soluble or water-insoluble forms (Skrovankova et al., 2015). Berries contain phenolic compounds such as resveratrol, anthocyanins, and chlorogenic acid in high concentrations (Häkkinen, 2000; Rodriguez-Mateos et al., 2012; Spinardi et al., 2019; H. Wang et al., 2017).

Total phenolic content

Postharvest UVC treatment increased total phenolic contents (TPC) in berries such as blueberries (González-Villagra et al., 2020; Nguyen et al., 2014), red raspberries (Gimeno et al., 2021), and strawberries (Amiri et al., 2021; Jin et al., 2017; Severo et al., 2015) during storage as shown in Table 3. For instance, UVC at 0.5 kJ/m^2 increased TPC by 47.75 % in strawberries (198.21 mg GAE/g fresh weight) compared to the control samples (103.97 mg GAE/g fresh weight) at the end of 12 d-storage (Amiri et al., 2021). Likewise, TPC in blueberries was increased by ~15 mg GAE/100 g fresh weight after UVC treatment at 6 kJ/m^2 compared to control samples (Nguyen et al., 2014).

Flavonoids (flavanols, flavonols, anthocyanins)

Berries have high levels of flavonoids, including anthocyanins, isoflavones, chalcones, flavonols, and flavones. These compounds are responsible for the biological activities, color, and aroma of fruit and have several effects on health (Del Rio et al., 2010; Devore et al., 2012). UVC treatment at 2 and 4 kJ/m^2 increased total flavonoid content (TFC) by 86.9 – 72 % in red raspberries during 12-d storage at 6 °C (Gimeno et al., 2021). Flavonol accumulation in blueberries was not affected by a UVC treatment at 2.76 kJ/m^2 (Yang et al., 2019).

Anthocyanins are a crucial group of flavonoids and are known as fruit colorants (Skrovankova et al., 2015). The flavylium cation (AH+) structure of anthocyanins makes them acidic pigments that give strawberry fruit its reddish color (pelargonidin-3-glycoside and cyanidin-3-glycoside) (Crecente-Campo et al., 2012; Wang and Zheng, 2001). The main characteristic of these substances is their capacity to scavenge free radicals (Tena et al., 2020). Amiri et al. (2021) showed that untreated strawberries' TAC was ~10 mg/100 g FW higher than the UVC-treated (0.5 kJ/m^2) ones during 12 d of storage. However, UVC treatment at 4 kJ/m^2 accelerated the increase of major anthocyanin compounds (pelargonidin-3-glucoside, cyanidin-3-glucoside-succinate, and cyanidin-3-glucoside at ranging from 232.8–302.3 mg kg^{-1}, 10.5–13.6 and 68.3–79.6, respectively) in fresh-cut strawberries during storage at 4 °C for 7 d (Li et al., 2019). Also, UVC treatment at range 2 and 4.35 kj/m^2 dose increased TAC in strawberries (M. Li et al., 2019; Severo et al., 2015) and red raspberries (Gimeno et al., 2021). (Xu and Liu, 2017) have reported that UVC treatment at 4 kJ/m^2 increased TAC from ~250 to 300 mg/100 g in blueberries stored at 4 °C for 8 d. Similarly, González-Villagra et al. (2020) have reported that UVC treatment at 4.6 kJ/m^2 increased TAC by 80 %, 50 %, and 20 % in 'Bluegold', 'Brigitta', and 'Legacy' blueberry cultivars, respectively, compared to control samples after 5-d storage. 'Bluecrop' blueberry cultivars' TAC levels were increased by 10 % after UVC treatments at 2 – 4 kJ/m^2, while the 'Collins' cultivars' TAC remained unaffected at the same doses and storage condition (7 d, 5 °C) (Perkins-Veazie et al. 2008). Furthermore, as reported by Wang et al. (2009), individual

anthocyanins (delphinidin-3-galactoside, cyanidin-3-galactoside, delphinidin-3-arabinoside, petunidin-3-galactoside, petunidin-3-glucoside, petunidin-3-arabinoside, malvidin-3-galactoside, malvidin-3-arabinoside) and flavonols (myricetin-3-arabinoside, quercetin-3-galactoside, quercetin-3-glucoside, kaempferol-3-glucuronide, kaempferol-3-glucoside) in UVC-treated (2.15, 4.30, or 6.45 kJ/m^2) blueberries were increased by up to 150 % compared to the untreated ones. Moreover, UVC treatment at 2.76 kJ/m^2 increased delphinidin, petunidin, cyanidin, peonidin, and malvidin in blueberries and activated anthocyanin biosynthesis during the postharvest term (Yang et al., 2018). Also, UVC treatment at the same dose (2.76 kJ/m^2) increased anthocyanin accumulation in immature (turning from green to purple and pink) and mature blueberries by 261.8 and 23.1 %, respectively, compared to control samples (Yang et al., 2019). Besides, UVC treatment activated genes responsible for flavonoid biosynthesis-related gene expression, including *Vaccinium corymbosum* leucoanthocyanidin reductase (*VcLAR)*, anthocyanidin reductase (*VcANR)*, and myeloblastosis proto-oncogene proanthocyanidin (*VcMYBPA1*) (Yang et al., 2019). These genes exhibit a high positive correlation with flavonol and proanthocyanins biosynthesis. Therefore, total flavonoids, flavonoid subgroups such as flavonols and anthocyanins, and related gene expressions were affected positively by UVC treatment (Table 3). The effects of UVC on the TAC depend on the dose and types of berries and their cultivars (Perkins-Veazie et al., 2008; Wang et al., 2009).

Table 3. Effect of postharvest ultraviolet C treatment on berries' phenolic compounds.
Tablo 3. Hasat sonrası ultraviyole-C uygulamasının dutsu meyvelerin fenolik bileşikler üzerindeki etkisi.

Berries	Wavelength	Dose (kJ/m^2)	Effects	References
Blueberry	254 nm	4	Increased TAC from ~250 to 300 mg/100 g and PAL activity	(Xu and Liu, 2017)
Blueberry	254 nm	2.76	Increased anthocyanin biosynthesis and associated genes, TAC by 196.4 and 40.8 % in turning (from green to purple and pink) and mature blueberries	(Yang et al., 2018)
Blueberry	254 nm	2.76	Unaffected flavonols (~ 0.5 g/kg FW) Increased anthocyanins by 261.8 and 23.1 % in turning (from green to purple and pink) and mature blueberries and proanthocyanidins (by 56 %)	(Yang et al., 2019)
Blueberry	254 nm	6	Increased TPC (by ~15 mg GAE/100 g FW), TAC (by ~88 mg/100 g), and individual anthocyanins	(Nguyen et al., 2014)
Blueberry	254 nm	2.3 and 4.6	Increased TPC (up to ~ 150%), TAC (by 80 %, 50 %, and 20 % depending on cultivars)	(González-Villagra et al., 2020)
Blueberry	254 nm	4	Increased PAL activity, TAC (by ~ 50 mg/100 g)	(Xu et al., 2016)
Blueberry	254 nm	2.15, 4.30, and 6.45	Increased chlorogenic acid from 40.6 ± 4.8 to 55.3 ± 6.8, 45.1 ± 6.1, and 46.0 ± 5.3 µg/g FW at 2.15, 4.30, and 6.45 kJ/m^2, respectively, and increased resveratrol (from 13.0 ± 0.7 to 17.4 ± 0.2 µg/g fresh weight)	(Wang et al., 2009)
Blueberry	254 nm	2 - 4	Increased 'Bluecrop' blueberry cultivars' TAC by 10 %, unaffected 'Collins' blueberry cultivars' TAC	(Perkins-Veazie et al. 2008)
Red raspberry	254 nm	2 and 4	Increased TPC at 4 d of storage, decreased TPC at 12 d of storage, increased TAC during 12 d of storage, and TFC (by ~87 – 72 %)	(Gimeno et al., 2021)
Strawberry	ND	4.1	Increased PAL activity	(Pombo et al., 2011)
Strawberry	254 nm	4.35	Increased TPC, TAC, individual phenolics (gallic acid, hydroxybenzoic acid, ρ-coumaric acid, quercetin and (+)-catechin), PAL and ANS activity	(Severo et al., 2015)
Strawberry	ND	2	Increased TPC, PAL activity	(Jin et al., 2017)
Strawberry	ND	0.5	Increased TPC from 103.97 to 198.21 mg GAE/g FW, decreased TAC	(Amiri et al., 2021)
Strawberry (Fresh-cut)	ND	4.0	Increased TPC (by ~ 0.12 g/kg), TAC (from 0.41 to 0.51 g/kg), individual phenolic compounds (*P*-coumaroyl glucose, kaempferol-3-glucoside, ellagic acid, ellagic acid glucoside), and anthocyanin compounds (pelargonidin-3-glucoside, cyanidin-3-glucoside-succinate and cyanidin-3-glucoside at ranging from 232.8 – 302.3 mg/kg, 10.5 – 13.6 and 68.3 – 79.6, respectively)	(Li et al., 2019)

ANS: anthocyanidin synthase, FW: fresh weight, ND: not determined, PAL: phenylalanine ammonia-lyase, TAC: total anthocyanin content, TFC: total flavonoid content, TPC: total phenolic content.

Non-flavonoids

Berries have non-flavonoids such as phenolic acids (benzoic acid and cinnamic acid derivates) and others (resveratrol, lignans, etc.) (Del Rio et al., 2010; Kaur et al., 2022; Smeds et al., 2012). UVC treatment at 4 kJ/m^2 increased *p*-coumaroyl glucose, ellagic acid, and ellagic acid glucoside in fresh-cut strawberries during 7-d storage at 4 °C (Li et al., 2019). Similarly, UVC treatment at 4 kJ/m^2 increased gallic acid, hydroxybenzoic acid, and *p*-coumaric acid in strawberries at 7 d storage at 20 °C (Severo et al., 2015). UVC treatments at 2.15, 4.30, or 6.45 kJ/m^2 increased chlorogenic acid in blueberries (55.3, 45.1, and 46.0 µg/g fresh weight, respectively), compared to the untreated ones (40.6 ± 4.8 µg/g fresh weight) (Wang et al., 2009). However, a lower UVC dose (0.43 kJ/m^2) did not affect the chlorogenic acid content (Wang et al., 2009). Besides, proanthocyanidins were increased by 56 % after UVC treatment at 2.76 kJ/m^2 in blueberries during postharvest storage (Yang et al., 2019). Non-flavonoids like hydroxybenzoic acid, *p*-coumaroyl glucose, ellagic acid, ellagic acid glucoside, and *p*-coumaric acid have anticarcinogenic, antibacterial, antiviral, antimutagenic, and anti-inflammatory properties (Mattila et al., 2006). Thus, UVC treatment can increase non-flavonoid contents and thus increase the biological activities of berries.

Enzymes involved in phenolic biosynthesis

Phenylalanine ammonia-lyase (PAL) is a key enzyme for increasing the biosynthesis of phenolic compounds such as flavonoids and anthocyanins (Deshi et al., 2020; Gimeno et al., 2021; Wen et al., 2008). PAL, as well as other enzymes such as chalcone synthase (CHS), flavanone 3-hydroxylase (F3H), leucoanthocyanidin reductase (LAR), anthocyanidin synthase (ANS), cinnamate-4-hydroxylase (C4H), 4-coumaroyl coenzyme A ligase (4CL), and stilbene synthase (STS), are responsible for biosynthesis of phenolic compounds and accumulating gene transcripts related to the pathways of phenolics (anthocyanins, resveratrol, etc.) (Gimeno et al., 2021; Sheng et al., 2018; J.-F. Wang et al., 2015). UVC treatment at 4 kJ/m^2 increased blueberry PAL activity by 2.7% compared to control after 8-d storage at 4°C (Xu and Liu, 2017). Similarly, UVC increased PAL activities in strawberries (Jin et al., 2017; Pombo et al., 2011; Severo et al., 2015). Li et al. (2019) also reported that UVC treatment activated PAL, 4CL, and C4H enzymes and their gene expression of *FaPAL*, *FaC4H*, and *Fa4CL* in strawberries compared to control. Moreover, PAL activities were promoted by a UVC treatment at 4.1 kJ/m^2 in strawberries, although anthocyanin accumulation was suppressed (Li et al. 2014). The authors argued that the suppression of anthocyanins might be due to the inhibition of 4CL and DFR enzymes by the UVC treatment. On the other hand, PAL, ANS, C4H, dihydro flavonol 4-reductase (DFR), chalcone isomerase (CHI), flavonoid 3-O-glucosyltransferase (UFGT) which are responsible for anthocyanin biosynthesis were not induced by UVC treatment in berries (Yang et al., 2018).

Overall, the studies show that UVC treatment increased phenolic compounds such as flavonoid and non-flavonoids, enzyme activities, and their relevant gene expression in berries (Table 3). The existing literature collectively shows that postharvest UVC treatment can increase phenolic compounds mainly anthocyanins by increasing PAL, ANS, and other biosynthesis enzymes in berries.

3.4. Antioxidant capacity

UVC treatment enhanced total antioxidant capacity in berries such as blueberries (Nguyen et al., 2014; Wang et al., 2009; Yang et al., 2019) and strawberries (Severo et al., 2015), possibly due to increased phenolic compounds, as shown in Table 4.

For instance, Amiri et al. (2021) showed that UVC at 0.5 kJ/m^2 caused a 29.9 % increase in the total antioxidant content of strawberries during storage. Besides, UVC treatment at 2 kJ/m^2 increased antioxidant enzymes such as catalase (CAT), ascorbate peroxidase (APX), and superoxide dismutase (SOD) in strawberries in comparison to the control group, during 12-d storage at 5 °C (Jin et al., 2017). Similarly, SOD activity in UVC-treated (at 4 kJ/m^2) fresh-cut strawberries increased by 39.5 % during storage (Li et al., 2019). Moreover, UVC treatment increased the activities of SOD, CAT, and APX enzymes involved in reactive oxygen species (ROS) metabolism in fresh-cut strawberries during 7-d storage at 4 °C (Li et al., 2019). However, SOD activity in blueberries was not affected by UVC treatment during 8-d storage at 4 °C (Xu et al., 2016). Accumulations of superoxide, hydroxyl, and hydrogen peroxide lead to oxidative stress in fruits. Increasing antioxidant enzymes (SOD, APX, and CAT) is important for reducing oxidative stress and tissue damage, and promoting cell survival (Jiang et al., 2010). As a result, postharvest UVC treatment at 0.5 – 6 kJ/m^2 maintained the total antioxidant capacity and their relative enzyme activities in berries.

3.5. Color

Berries' visual appeal is primarily due to their color formed through chlorophyll degradation and pigment synthesis. Berries are rich in anthocyanins commonly known as fruit colorants (red-blue-purple) (Skrovankova et al., 2015). Enzymes such as peroxidase (POD) and polyphenol oxidase (PPO) are responsible for enzymatic browning reactions in fruit during the postharvest storage period, causing color changes (Costa et al., 2021). Jin et al. (2017) demonstrated that UVC treatment at 2 kJ/m^2 increased the POD and PPO activities in strawberries by ~60 and 38.7 %, respectively, after 12-d storage at 5 °C and 90–95 % relative humidity. Increasing PPO and POD with UVC treatment might cause enzymatic browning and discoloration. However, UVC treatment at 4 kJ/m^2 inhibited the POD activity of blueberries by 10.2 % end of 8-d storage at 4 °C (Xu and Liu, 2017).

The International Commission on Illumination (CIE) – L*a*b* color space system is used in determining the color characteristics of berries quantitatively using L* (lightness), a* (greenness to redness), and b* (blueness to yellowness) values (Markovic et al., 2013). These parameters are determined by the chemical and physical changes in the product and show the visual color quality important for the sensory perception of products. UVC treatment at 4 kJ/m^2 caused no systematic changes in the a* and b* values of strawberries (Li et al., 2014), blueberries (Xu et al., 2016; Xu and Liu, 2017), and red raspberries (Gimeno et al., 2021) during postharvest storage. For instance, the L* value of blueberries was unaffected by a UVC treatment at 4 kJ/m^2 (Xu and Liu, 2017), while the UVC treatment at the same dose caused an increase in the L* value of strawberries (Li et al., 2014). Besides, as mentioned earlier, numerous studies showed that anthocyanin, which is responsible for red, purple, and blue colors, was increased by UVC treatment. Overall results might be concluded that exposure to UVC treatment could preserve berries' color and increase anthocyanin levels and PAL activity, although PPO and POD activities were also increased.

Table 4. Effect of postharvest ultraviolet-C treatment on berries' antioxidant capacity.
Tablo 4. Hasat sonrası ultraviyole-C uygulamasının dutsu meyvelerin antioksidan kapasitesi üzerindeki etkisi.

Berries	Wavelength	Dose (kJ/m^2)	Effects	References
Blueberry	254 nm	4	Unaffected antioxidant enzymes activities (SOD; ~190 U/g FW)	(Xu et al., 2016)
Blueberry	254 nm	6	Increased antioxidant activities	(Nguyen et al., 2014)
Blueberry	254 nm	4.6	Increased antioxidant properties and radical scavenging activity	(González-Villagra et al., 2020)
Blueberry	254 nm	2.76	Increased antioxidant capacity and their enzyme activity (SOD) (39.5 %)	(Yang et al., 2019)
Red raspberry	254 nm	2 and 4	Increased antioxidant activity	(Gimeno et al., 2021)
Strawberry	ND	0.5	Increased antioxidant activity (29.91 %) and L-ascorbic acid content	(Amiri et al., 2021)
Strawberry	ND	2	Increased antioxidant enzymes activities (SOD, CAT, APX)	(Jin et al., 2017)
Strawberry	254 nm	4.35	Increased antioxidant activity	(Severo et al., 2015)
Strawberry (Fresh-cut)	ND	4.0	Increased antioxidant capacity	(Li et al., 2019)

APX: ascorbate peroxidase, CAT: catalase, FW: fresh weight, ND: not determined, SOD: superoxide dismutase

3.6. Flavor

The free sugar content, total soluble solids (TSS), and titratable acidity (TA) are crucial parameters for flavors and sensory properties of berries. The effect of UVC treatment on flavor in berries is shown in Table 5**.** UVC treatment decreased sugar (fructose and glucose) (Yang et al., 2018) and total soluble sugar (González-Villagra et al., 2020) in berries, while unaffecting TSS and TA in berries such as strawberries (Amiri et al., 2021) and blueberries (González-Villagra et al., 2020). During storage, strawberries' TSS content increased from 6.73 % to 7.93 % but UVC inhibited this increase in the first 3 d (Li et al., 2014). Furthermore, UVC treatment at 4.35 kJ/m^2 increased the synthesis of the aroma-producing ester volatiles such as alcohol dehydrogenase (*ADH*) and alcohol acetyltransferase (*AAT*) transcript accumulation in strawberries (Severo et al., 2015). Li et al. (2019) reported that UVC exposure at 4 kJ/m^2 suppressed the increase of sour, bitter, and astringent tastes of fresh-cut strawberries. On the other hand, PPO and POD are responsible for off-flavor and off-odor in fruit during the postharvest storage period (Costa et al., 2021). Jin et al. (2017) found that UVC treatment at 2 kJ/m^2 increased POD and PPO activities in strawberries by ~60 % and 38.7 %, respectively, however, it inhibited blueberries' POD activity by 10.2 % at 4 kJ/m^2 during 12-d storage at 5°C.

Table 5. Effect of postharvest ultraviolet-C treatment on berries' flavor.
Tablo 5. Hasat sonrası ultraviyole-C uygulamasının dutsu meyvelerin lezzeti üzerindeki etkisi.

Berries	Wavelength	Dose (kJ/m^2)	Effects	References
Blueberry	254 nm	4	Inhibited soluble solid content	(Xu et al., 2016)
Blueberry	254 nm	2.76	Decreased sugar (fructose and glucose) and total soluble sugar	(Yang et al., 2018)
Blueberry	254 nm	4.6	Unaffected TSS and TA	(González-Villagra et al., 2020)
Strawberry (Fresh-cut)	ND	4.0	Decrease of increase of sourness, bitterness, and astringency tastes Increased volatile compounds	(Li et al., 2019)
Strawberry	ND	0.5	Unaffected TA	(Amiri et al., 2021)
Strawberry	ND	4.1	Decreased TSS	(Li et al., 2014)
Strawberry	254 nm	4.35	Increased aroma-producing ester volatiles and *ADH* and *AAT* transcript accumulation	(Severo et al., 2015)
Blueberry	254 nm	4	Inhibited soluble solid content	(Xu et al., 2016)
Blueberry	254 nm	2.76	Decreased sugar (fructose and glucose) and total soluble sugar	(Yang et al., 2018)

AAT: alcohol acetyl transferases, ADH: alcohol dehydrogenase, ND: not determined, TA: titratable acidity, TSS: total soluble solids

3.7. Microbial Decay

Postharvest microbial decay, primarily caused by *Botrytis cinerea, Rzihopus,* and *Colletotrichum*, significantly affects the shelf life of berries, making them highly susceptible to spoilage (Kumar et al., 2018). Several studies have been conducted on the effects of UVC treatment on microbial decay in berries, as shown in Table 6. Xu and Liu (2017) showed that blueberry decay incidence was suppressed by UVC treatment at 6 kJ/m^2 compared to control, during 8-d storage at 4 °C. Zhou et al. (2019) indicated that decay incidence in UVC-treated blueberries at 2.67 kJ/m^2 (~17.69 %) was lower than that in the control (~35.49 %) after 8-d storage. Similarly, the incidence of rot in red raspberries was inhibited by 15 – 20 % upon UVC treatment at 2 and 4 kJ/m^2 after 12-d storage at 6 °C (Gimeno et al., 2021). Besides, UVC at 0.5 – 2 kJ/m^2 effectively inhibited gray mold decay in strawberries inoculated with *B. cinerea* (Amiri et al., 2021; Jin et al., 2017). Jin et al. (2017) also found that strawberries treated by UVC at 2 kJ/m^2 had a 36.1 % and 24.2 % reduction in *B. cinerea* lesion diameter after 9- and 12-d storage, respectively, at 5 °C. Adhikari et al. (2015) found that higher UVC-induced inactivation rates were observed in fruits with smoother and less hydrophobic surfaces (apples and pears) compared to the ones in fruits with rougher surfaces such as strawberries and raspberries. Thus, surface characteristic is a critical factor for UVC efficiency.

Table 6. Effect of postharvest ultraviolet-C treatment on berries' microbial decay.
Tablo 6. Hasat sonrası ultraviyole-C uygulamasının dutsu meyvelerin mikrobiyal çürüme üzerindeki etkisi.

Berries	Wavelength	Dose (kJ m^{-2})	Effects	References
Blueberries	254 nm	4	Decreased decay incidence	(Xu and Liu, 2017)
Blueberries	254 nm	6	Reduced decay	(Nguyen et al., 2014)
Blueberry	275 nm (UVLED)	0.16	0.91–0.95 log reduction *Escherichia coli*	(Haley et al., 2023)
Blueberry	ND	2.67	Reduced decay incidence and *Botrytis cinerea,* total aerobic mesophilic bacteria, total mold and yeast	(Zhou et al., 2019)
Blueberry	254 nm	<11.4	Delaying and reducing *B. cinerea* and fungal infection	(Jaramillo Sánchez et al., 2021)
Blueberry	254 nm	4	Inhibited decay incidence	(Xu et al., 2016)
Blueberry (in water)	254 nm	9.5 – 47.4	< 5.2 log reduction *E. coli* O157:H7	(C. Liu et al., 2015)
Raspberry	254 nm	10.5	Reduction of 1.1 log *E. coli* and 1 log *Listeria monocytogenes*	(Adhikari et al., 2015)
Red raspberries	254 nm	2 and 4	Reduced rot incidence and total aerobic mesophilic bacteria, total mold and yeast	(Gimeno et al., 2021)
Strawberry	ND	2	Inhibited gray mold decay by *B. cinerea*	(Jin et al., 2017)
Strawberry	ND	0.5	Decreased decay *B. cinerea*	(Amiri et al., 2021)
Strawberry	254 nm	7.2 and 11.9	Reduction of 2 log *E. coli and* 1 log *L. monocytogenes*	(Adhikari et al., 2015)
Strawberry (Fresh-cut)	ND	4.0	Reduced microbial growth and total aerobic bacterial count	(M. Li et al., 2019)

ND: not determined

UVC treatment also had a significant impact on the safety of berries through inactivating human pathogens. Berries are highly susceptible to microbial contamination. Thus, several studies have evaluated UVC's effectiveness in inactivating human pathogens in berries. For instance, Haley et al. (2023) showed that UVC treatment at 0.16 kJ/m^2 and 275 nm caused up to 0.95-log inactivation in *E. coli* on blueberries. UVC treatment at higher doses (9.5 – 47.4 kJ/m^2) and 254 nm decreased *E. coli* O157:H7 count by 5.2-log in another study (Liu et al., 2015). A 2-log reduction in *E. coli* and a 1-log reduction in *L. monocytogenes* were obtained by UVC treatment at 7.2 and 11.9 kJ/m^2 in strawberries (Adhikari et al., 2015).

The inhibition of pathogens and microbial decay can also be related to increasing phenolic compounds and antioxidants (Amiri et al., 2021; Jin et al., 2016; Nigro et al., 2000). In addition, PAL, chitinases, and β-1,3-glucanases are also known as defense-related enzymes against pathogens (Abd El-Rahman et al., 2012; Nigro et al., 2000; Pombo et al., 2009). Chitinase hydrolyzes fungal cell wall chitin and β-1,3-glucanase releases the oligosaccharides pathogen microorganism cell walls. After UVC treatment, their activity and relevant gene (*CCR-1 allele, CAT, CHI2, PPO,* and *PLA6*) expression were induced (Jin et al., 2017; Sheng et al., 2018). Thus, these enzymes, phenolic compounds, and antioxidants that are induced by UVC treatment might also be associated with inhibition of microbial decay and relevant microorganisms in berries. Therefore, overall results indicate that UVC treatment effectively inhibits microbial decay, inactivates pathogens, and enhances disease resistance against gray mold in berries.

4. Effects of UVC combined with other applications on berries' physiology

Cold storage (Amiri et al., 2021; Nguyen et al., 2014; Ortiz Araque et al., 2019), edible coating (Mannozzi et al., 2017), *Aloe vera* gel (Sempere-Ferre et al., 2022), and active packaging (Chiabrando et al., 2019) have been studied to extend shelf life of berries. UVC treatment has been studied as a non-thermal and non-chemical treatment for extending shelf life (Green et al., 2020; Rabelo et al., 2020; Zhai et al., 2021). Although postharvest UVC treatment has several advantages like decreasing weight loss, inhibiting microbial decay, and increasing phenolic compounds, antioxidant capacity, and firmness, it can cause increased respiration rate and ethylene production, and insufficient surface decontamination in berries. Consequently, other physical or chemical treatments combined with UVC treatments have been studied, as shown in Table 7**.** For instance, Xu and Liu (2017) conducted UVC treatment combined with 1-methylcyclopropene (1-MCP), which is commercially used to inhibit the ethylene action in climacteric fruits. The combination of the two treatments showed better results in maintaining the quality and extending the shelf life of blueberries compared to using 1-MCP or UVC treatments alone. Also, the combined treatment decreased ethylene production in blueberries by 5.9 % and exhibited higher TAC values than the control and individual treatments during 8-d storage at 4 °C (Xu and Liu, 2017). Gimeno et al. (2021) reported that a combination of passive modified atmosphere packaging (MAP) and UVC (254 nm at 4 kJ/m^2) treatment in raspberries effectively delayed senescence, prolonged shelf life, and increased bioactive compounds. Aqueous chlorine dioxide (ClO_2) and UVC combination inhibited microorganism growth, delayed maturity and senescence, and extended the shelf-life of blueberries (Xu et al., 2016). The efficiency of combined treatment was higher than individual treatments (UVC or ClO_2). Li et al. (2014) indicated that 1 mM abscisic acid (ABA) combined with UVC treatment (4.1 kJ/m^2) significantly enhanced antioxidant capacity in strawberries. The strawberries treated with the combined ABA and UVC produced less ethylene than those treated with UVC alone. Mild heat treatment (45 °C, 3 h in air) and UVC combination had higher effects on delaying spore germination of *B. cinerea* in *in-vitro* assays compared to each treatment alone (Pan et al., 2004). Also, Marquenie et al. (2003) showed that pulsed white light (30 µs pulses, 15 Hz, 40 to 250 s) combined with UVC at 1 kJ/m^2 increased the inactivation *Monilia fructigena* and *B. cinerea* in strawberries, compared to UVC alone. As a result, combining UVC with additional treatments (mild heat treatment, pulsed white light, ClO_2, ABA, MAP, 1-MCP) may lead to improved postharvest preservation of berries.

Table 7. Effect of postharvest ultraviolet-C treatment and other combined applications on berries' physiology.
Tablo 7. Hasat sonrası ultraviyole-C uygulamasının ve diğer kombine uygulamaların dutsu meyvelerin fizyolojisi üzerindeki etkisi.

Berries	Treatments with combination UVC	Combination effects	References
Blueberry	Aqueous chlorine dioxide (ClO_2)	-inhibited microbial growth, respiration rate, weight loss, decay incidence -delayed maturity, senescence, and decline of firmness, color -maintained shelf-life quality, anthocyanin content	(Xu et al., 2016)
Blueberry	1-methylcyclopropene (1-MCP)	-maintained quality -extended shelf life -inhibited respiration rate, ethylene production, decay incidence, POD activity -delayed softening -increased total anthocyanin content	(Xu and Liu, 2017)
Raspberry	Modified atmosphere packaging (MAP) film	-delayed senescence -prolonged shelf life -maintained bioactive compounds	(Gimeno et al., 2021)
Strawberry	Abscisic acid (ABA)	-enhanced antioxidant capacity -decreased ethylene production compared to UVC alone	(Li et al., 2014)
Strawberry	Heat treatment	- decreased total sugar content (slightly) -delayed spore germination of *B. cinerea*	(Pan et al., 2004)
Strawberry	Pulsed white light	-increased inactivation of *Monilia fructigena* and *B. cinerea*	(Marquenie et al., 2003)

5. Conclusion

UVC treatment is an effective, simple, and eco-friendly method for preserving berry physiologies including reducing weight loss, inhibiting cell wall metabolism, enhancing antioxidant capacity and biosynthesis enzymes such as SOD, APX, and CAT, and increasing phenolic compounds (flavonoids, non-flavonoids, and their synthesis enzymes such as PAL, ANS, etc.). Besides, it has great potential to inhibit microbial decay, inactivate pathogens, and enhance disease resistance against gray mold in berries caused by *B. cinerea*. However, UVC treatment can cause increasing PPO and POD, thereby causing enzymatic browning and degradation of flavor. In addition, UVC treatment might increase respiration rate and ethylene production, causing rapid senescence and flavor degradation. On the other hand, UVC doses, berry types, and other processing parameters are all important parameters for UVC efficiency. Furthermore, combining UVC treatment with other chemical and physical techniques like cold storage, 1-MCP, MAP, ABA, and pulsed white light has increased the efficiency of the control of berries' postharvest physiology compared to UVC treatment alone. Thus, the hurdle approach could be more effective for berries postharvest term. Future research may focus on the commercial applicability of the UVC technology alone or in combination with other treatments for controlling berries' physiology. In addition, more research needs to be conducted to understand the effects of UVC exposure on berries' sensory evaluation, ethylene production, and respiration rates.

6. Conflicts of Interest

The authors declare no conflict of interest.

7. References

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