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Effects of Abiotic Stress (UV-C) Induced Activation of Phytochemicals on the Postharvest Quality of Horticultural Crops

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1. Introduction

Phytochemicals are bioactive non-nutrient plant components that have gained considerable attention as photoprotective agents in providing certain health benefits and are well known for their powerful antioxidant and free radical scavenging potential [1-2, 8]. Phytochemicals found in plant-based foods (fruits, vegetables, legumes, nuts, cereals, and grains) belong to several classes according to their chemical structures and physiological functions and include polyphenols, flavonoids, isoflavonoids, phytoalexins, phenols, anthocyanidins, nitrogen compounds (polyamines), chlorophyll derivatives, beta carotene (pro-vitamin A), and other carotenoids, ascorbic acid (vitamin C), folic acid, and α -tocopherol (vitamin E). Figure 1 illustrates the classification of dietary phytochemicals, which are widely distributed with different structures at the tissue, cellular, and sub-cellular levels. While it has been reported that there are over 4,000 phytochemicals, the most studied are the phenolics (largest category of phytochemicals) and carotenoids [3, 5], whereas some phytochemicals are distributed only among limited taxonomic groups. For example, glucosinolates are only found in the cruciferous vegetable crops, whereas the occurrence of sulfides is restricted to the Liliaceae. Additionally, each fruit and vegetable species has a distinct profile of phytochemicals, which is also within a special phytochemical group [4]. Many phytochemicals, particularly the pigment molecules, are often concentrated in the outer layers of the various plant tissues [5]. Some sources of phytochemicals include lycopene from tomatoes, isoflavones from soy, β -carotene from carrots, and anthocyanins from blueberries and grapes. The phytochemicals lutein and zeaxanthin are carotenoids found in spinach, kale, and turnip greens. Another group of phytochemicals called allyl sulfides are found in garlic and onions. <http://www.cancer.org/treatment/treatmentsandsideeffects/complementaryandalternativemedicine/herbsvitaminsandminerals/phytochemicals>

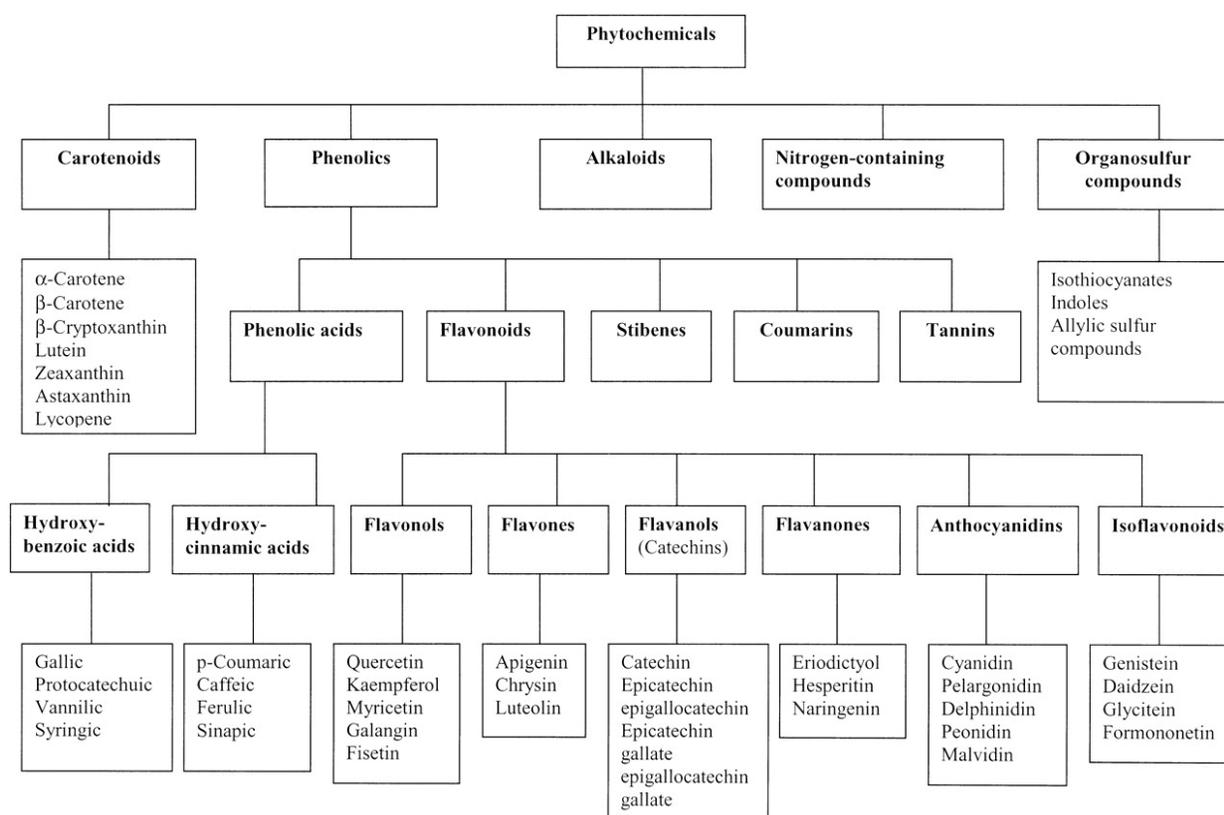


Figure 1. Classification of dietary phytochemicals (Adapted from [3]).

The beneficial effects of phytochemicals are mediated through several mechanisms that include enzyme stimulation, interference with DNA replication, anti-bacterial effect, and physical action. Enhancing the health benefits of fresh produce through physical methods could therefore add value and create new opportunities for growers and processors by tapping into health-oriented markets [12, 57]. Abiotic stresses (negative impact of non-living environmental factors on growth and productivity of crops) are significant determinants of quality and nutritional value of crops along the food value chain. While abiotic stress is essentially unavoidable, simple modifications to postharvest handling systems may result in significant reduction in stress exposure, which will positively impact on phytochemical content and storage and/or shelf-life extension [7, 10]. There is a need to provide technologies that can ensure the delivery of high-quality products with high levels of the desired phytonutrients [6, 11-12, 15]. There is now considerable literature on the use of low dose UV-C radiation to control postharvest pathogens, delay postharvest senescence, and improve shelf-life of many horticultural crops. It also has potential for commercial use as a surface treatment in the food industry, particularly for whole and fresh-cut produce. However, the use of UV-C radiation as an elicitor of phytochemicals which enhances additional health benefits and mechanisms related to improvement in shelf-life or increase in the content of phytonutrients are still not well understood. The objective of this chapter will focus on a review of recent studies of UV-C abiotic stress on the production and activation of phytochemicals and its effect on the quality of crops.

2. UV radiation and its interactions with biological systems

UV radiation is generally divided into three classes: UV-C (200-280 nm), UV-B (280-320 nm), and UV-A (315-400 nm) [21]. Each band can induce significantly different biological effects in plant systems. UV-C wavelengths (highly energetic) result in high levels of damage very quickly [22]; however, such radiations are effectively absorbed by ozone and atmospheric gases and are not present in sunlight at the earth's surface. UV radiation below 320 nm is actinic, which means it causes photochemical reactions [21]. Such reactions occur as a result of the absorption of photons by chromophores (chemical grouping of molecules) at particular wavelengths.

2.1. Direct and indirect effects of UV radiation

The destructive action of UV radiation results from both direct absorption of photons by DNA and indirect mechanisms involving excitation of photosensitizers and the generation of reactive oxygen species (ROS). Nucleic acids, proteins, lipids, indole acetic acids, flavor-proteins, and phytochromes are molecules that contain conjugated double bonds and absorb energy in the UV region. They have key roles in plant cell function and structure and any alterations of these compounds due to UV radiation might be expected to cause physiological alterations in crops. Plants may differ in resistance to ROS depending upon the efficiency of the plant defense systems that involve DNA repair systems and quenching systems involving either a suppression of ROS production or scavenging of ROS, which have already been produced with enzymatic and non-enzymatic scavenging pathways. This can affect the secondary metabolism of fresh produce and increase the synthesis of phytochemicals or reduce the synthesis of undesirable compounds [4, 12, 16]. The biological consequences of free radical reactions leading to cellular dysfunction and cell death are summarized in Figure 2.

3. Postharvest abiotic stress and the production of phytochemicals

Harvested crops can be potentially exposed to various abiotic stresses that impact on quality in the food value chain. These include qualitative and quantitative losses including sensorial, microbial, and nutritional losses [7]. Wide variation in resistance to stress injury exists in higher plants and the stress tolerance threshold are determined by plant species, the developmental stage of the plant, type of stressor, exposure time, as well as other factors such as the plant stress-coping mechanisms. Abiotic stresses play a major role in determining the distribution of plant species across different types of environments. Many breeding programs impose abiotic stresses on the plants in a very quantitative way to develop stress tolerance that will allow crops to adapt to climate change [10]. However, it is not clear whether breeding in the field will also extend stress resistance characteristics in the postharvest phase including shelf-life extension and phytonutrient quality of crops.

Various abiotic stresses (salinity, water stress, drought, heavy metals, wind, air pollution, altered gas composition, light, temperature extremes, and exposure to ultraviolet or gamma

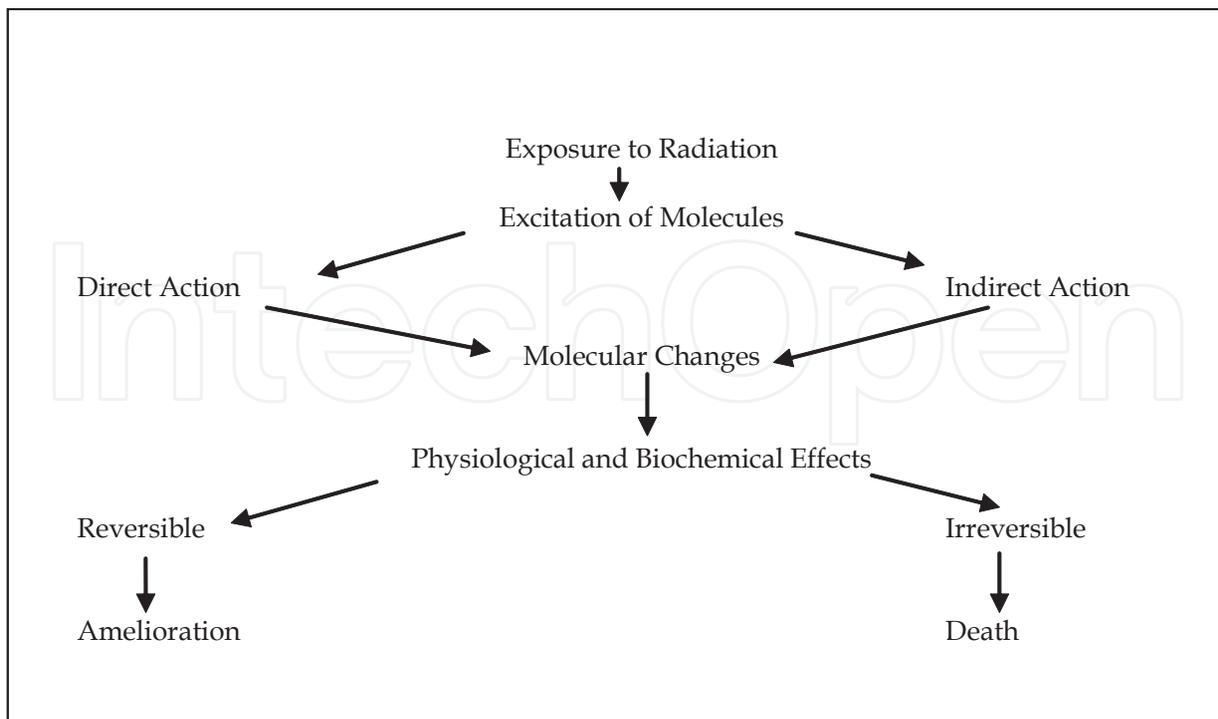


Figure 2. Schematic representation of the photobiological effects of UV-C radiation in plants [26].

radiation) are known to have deleterious effects on plant tissues as a result of the production of ROS, causing progressive oxidative damage, which can damage biomolecules and may affect biochemical pathways, leading to cell death (as shown in Figure 2) and cause substantial crop losses worldwide [13, 16, 18-19]. Postharvest abiotic stressors can lead to numerous quality problems in fruits and vegetables, including scald, core and flesh browning of fruits, sweetening, pitting, water-soaked appearance, abnormal ripening, russeting, tissue softening, and loss of nutrient constituents [10]. Hence an understanding of the effects of field abiotic stresses on postharvest stress susceptibility will become more important since postharvest stresses limit the storage and shelf-life potential of crops. Characterization of mutants and transgenic plants with altered expression of antioxidants is also a potentially powerful approach to understanding the functioning of the antioxidant system and its role in protecting plants against stress [6, 13]. The use of genetically modified crops has its biases as in most cases it is considered as potential biological hazards that create an ecological imbalance [6, 9].

As a secondary response, some postharvest abiotic stress treatments could induce some mechanisms that affect the metabolic activity of the treated produce, such as triggering antioxidants. Studies have shown that plants with higher levels of antioxidants, whether constitutive or induced, showed a greater resistance to different types of environmental stresses [13]. Plants possibly protect themselves against increased UV irradiation by an increased synthesis of pigments in the epidermis [23]. However, the mechanisms of cellular oxidative stress are complex, and other biochemical and physiological mechanisms may act in concert under UV stress. Figure 3 illustrates possible mechanisms for using controlled postharvest abiotic stresses to enhance the phytochemical content of crops [7].

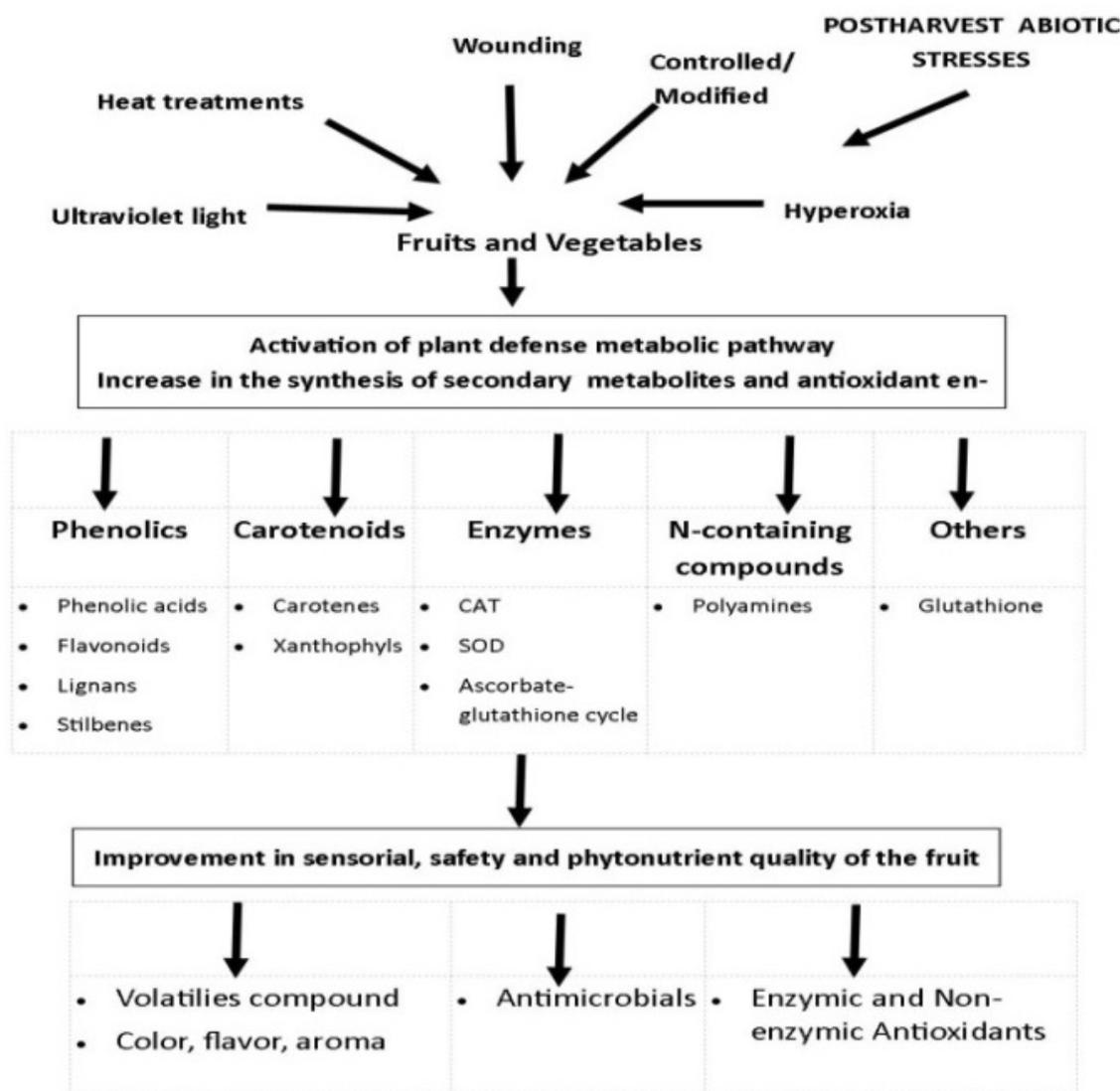


Figure 3. Effect of postharvest abiotic stress on the production of phytochemicals (adapted from [7]).

4. UV-C as a postharvest treatment

Non-ionizing artificial UV-C irradiation is a postharvest treatment that can be adjunct to refrigeration for delaying postharvest ripening, senescence, and decay in different fruit and vegetable species. UV-C radiation is mainly used as a surface treatment because it penetrates only 5-30 microns of the tissue and is beneficial for keeping the integrity and freshness of fruits and vegetables [27, 65]. It has been extensively used for many years in the disinfection of equipment, glassware, and air by food and medical industries. Exposure to abiotic UV-C radiation stress is well known to have deleterious effects on plant tissues however low levels may stimulate beneficial responses of plants, a phenomenon known as Hormesis [14, 28]. The use of UV-C hormesis to improve the postharvest quality of fresh fruits and vegetables has

been the subject of numerous research activities during the last two decades, with some early applications in the eighties on the control of postharvest pathogens. UV-C doses above the optimal level can lead to detrimental color development and poor appearance of fruits and vegetables, thus lowering aesthetic value and lead to poor marketability of such treated produce [15]. Turtoi [27] and Ribeiro [11] conducted recent reviews on the effects of UV-C primarily on decontamination and disease control in fresh fruits and vegetables. UV-C irradiation also holds considerable promise as a non-chemical treatment to delay ripening and senescence and to improve shelf-life of fresh fruits and vegetables and the associated health and therapeutic benefits with their consumption [11, 28]. In a more recent study, UV-C hormesis was induced at the pre-harvest stage, which has commercial implications particularly for crops that are easily damaged during postharvest treatment [20]. UV-C treated crops, with the ability to scavenge and/or control the level of cellular ROS with the consequential activation of phytochemicals may be useful to improve postharvest storage life and enhance nutritional quality and health benefits. However, the reported biochemical and molecular mechanisms of such effects are complex and quite diverse and depend on several factors such as differences in crops sensitivity, maturity levels, UV-C doses, equipment, and environmental conditions as previously noted.

4.1. UV-C technology

UV-C irradiation can be applied using low and medium pressure mercury vapor discharge lamps with a peak emission at 254 nm inside an enclosed chamber that is kept closed during irradiation. The lamps are suspended directly over the sample in the chamber at a fixed distance from the sample and radiation doses are varied using different exposure times. The intensity of the light is affected by the distance the source is from the sample. Manual rotation is generally employed to the treated commodity to ensure irradiation uniformity. The use of devices to rotate the crops to ensure radiation uniformity is noted in [20]. The dose is calculated from the product of exposure time and irradiance, as measured by portable handheld digital radiometers. The irradiance, sometimes called intensity, has the preferred units of mWcm^{-2} while the UV dose has the preferred units of kJm^{-2} [21]. UV dose may be calculated from the following formula:

$$D = I (T)$$

where D = dosage, I = applied intensity, and T = time of exposure.

There are several advantages in the use of UV-C technology such as:

- it leaves no residues after treatment, including moisture residues,
- it does not involve complex expensive equipment,
- it is simpler and more economical to use than ionizing radiation, and
- it generally lacks regulatory restrictions.

The beneficial effects from UV-C radiation result from the use of very low UV doses ranging from 0.125 kJm^{-2} to 9 kJm^{-2} and the time scale for the induction of such effects is generally

measured over hours (h) or even days [11, 15, 17]. The design of UV-C equipment and technology on a commercial scale for fresh fruits and vegetables and fresh-cut food industry poses a challenge with respect to ensuring affordable technology and simultaneously protecting operators from harmful effects of UV-C rays while effectively treating fruit tissue to ensure significant and consistent microbial load reduction and activation of beneficial phytochemicals.

5. UV-C radiation and its effects on phytochemicals

Plants possess a variety of phytochemicals to protect against the adventitious production of ROS caused by specific postharvest elicitor treatments [4, 13]. Such phytochemicals include the enzymes superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), glutathione reductase (GR), polyphenol oxidases (PPO), guaiacol peroxidase (GPX), as well as water and fat-soluble antioxidants (ascorbic acid, thiol containing compounds, tocopherols, carotenes) and general antioxidants such as phenolic compounds. Non-enzymic phytochemicals play a significant role in protecting the cell from oxidative stress that occurs when there is a disturbance between the production of free radicals and antioxidant defenses [13, 18, 24]. A summary of some changes in enzymic and non-enzymic phytochemicals in postharvest UV-C treatment of some crops are illustrated below.

5.1. Enzymic phytochemicals

5.1.1. Superoxide Dismutase (SOD), Glutathione Reductase (GR), Catalase (CAT)

SOD is a ubiquitous defensive enzyme against superoxide damage to aerobic organisms. SOD catalyzes the dismutation of the one-electron reduced form of oxygen ($O_2^{\cdot-}$) or superoxide radical resulting in the production of the less toxic hydrogen peroxide and oxygen: $2 O_2^{\cdot-} + 2H^+ \rightarrow H_2O_2 + O_2$ [18, 25]. The H_2O_2 formed by the action of SOD is itself a strong oxidant and is toxic to cells. It can then be converted to oxygen and water in consecutive reactions with ascorbate and glutathione or with CAT in plant tissues [20]. SOD activity and enzymes of the H_2O_2 scavenging pathway are induced by diverse environmental stresses. High SOD activity has been reported to increase in plants exposed to various stresses [18]. GR is a key enzyme in the glutathione-ascorbate cycle and can regenerate reduced glutathione from its oxidized form. Together with glutathione, it is an important component of the ROS scavenging system in plant cells. GR has its main function as a detoxifier of peroxide from the cells. Peroxide decomposes to form highly reactive free radicals which can damage proteins, DNA and lipids. CAT a high capacity but low affinity enzyme destroys H_2O_2 and promotes the redox reaction: $2H_2O_2 \rightarrow 2H_2O + O_2$. This enzyme has been reported to show a general decline in activity with increasing illumination, with degradation exceeding the capacity for repair [13]. In one study, activities of SOD, GR, and CAT were more than 2-fold higher during the first 1 h after UV-C treatment of peanut seedling [38]. Overall, the general trend is that UV-C stressed crops show an initial increase in enzyme activity followed by a decrease in the antioxidant enzymes.

Table 1 summarizes the changes in SOD, GR, and CAT activities with postharvest UV-C treatment of some crops.

Crop	UV-C conditions	Results	Source
Banana (cv. Cavendish)	0.02 kJm ⁻² , 0.03 kJm ⁻² and 0.04 kJm ⁻² and storage at 5°C and 25°C for 7 days and 21 days	SOD activity in both control and UVC-treated fruit decreased with storage time, with a slight increase at the end of storage, but UV-C treated fruit maintained higher SOD activity throughout storage. UV-C treatment led to significantly higher activities of SOD, CAT, POD, APX, and GR compared to control fruit during later storage.	[30]
Yellow Bell Pepper	2.2 kJm ⁻² , 4.4 kJm ⁻² , and 6.6 kJm ⁻² and storage at 12 ± 1°C for 15 days	UV-C illumination at 6.6 kJm ⁻² enhanced the activities of enzymes such as CAT, SOD, GPX, and APX in yellow bell pepper during storage when compared to control fruit.	[32]
Pear (cv. Yali)	5 kJm ⁻² and storage at 20°C for 42 days	Activities of SOD, GR, and CAT in Yali pear fruit were significantly enhanced with UV-C dose compared to control fruit even up to the end of the storage period.	[33]
Strawberry	0.43 kJm ⁻² , 2.15 kJm ⁻² , and 4.3 kJm ⁻² and storage at 10°C for 15 days	Total SOD activity decreased in both control and UV-C treated strawberries, but after 15 days of storage all UV-treatments showed higher SOD levels than controls. UV-treated fruits at 2.15 kJm ⁻² dose (5 min) had the highest GR activity. GR activity increased during the first 10 days of storage and then declined after 15 days of storage.	[34]
Strawberry	0.25, 0.5 kJm ⁻² and 0.75 kJm ⁻² and storage at 10°C for 15 days	SOD activity increased at day 5 but then declined during storage. Extracts from all UV-C treated fruits had higher SOD activities compared to control fruits during storage. UV-C doses at 0.5 kJm ⁻² and 0.75 kJm ⁻² enhanced SOD and CAT activities in fruit after 5 days but levels declined after.	[35]
Tomato (cv. Capello)	3.7 kJm ⁻² and 24.4 kJm ⁻² and storage at 16°C for 28 days	SOD levels were lowest at day 0 and increased during the pre-climacteric phase attaining a maximum level by day 14 for control and day 21 for UV-C treated fruits (both doses) prior to declining in the post-climacteric phase. SOD levels were generally lower for UV-C treated fruit than controls.	[36]
<i>Turnera diffusa</i> Willd (<i>Damiana</i> medicinal plant)	0.38 mWcm ⁻² ; 5, 10, and 20 min day ⁻¹ and storage for 10 days	No significant differences were found in SOD activity of <i>damiana</i> leaves between UV-C treatments and control plants.	[37]
Fresh-cut watermelon	1.6, kJm ⁻² , 2.8 kJm ⁻² , 4.8 kJm ⁻² , and 7.2 kJm ⁻² and storage at 5°C for 11 days	The general trend in CAT activity was a decline from initial values however the 1.6 kJm ⁻² and 4.8 kJm ⁻² treatments kept the initial activity of this enzyme throughout shelf-life.	[39]

Table 1. Summary of changes in SOD, GR, and CAT activities with postharvest UV-C treatment of crops.

5.2. Non-enzymic phytochemicals

5.2.1. Phytoalexins

Resistance to infection by pathogen or abiotic stress is correlated with the induction of plant defense mechanisms and this is manifested through the stimulation of anti-microbial compounds such as phytoalexins. Allixin was the first compound isolated from garlic as a phytoalexin and a possible compound for cancer prevention. Trans-resveratrol produced by a large number of plants has a wide range of beneficial biological properties including being attributed with a relatively low incidence of cardiovascular disease and associated with reduced cancer risk [8]. A more detailed review of the stilbene resveratrol in grape and grape products irradiated with UV-C can be found in [8] and in peanuts [38, 43]. Resveratrol was present in substantial amounts (1.2-2.6 $\mu\text{g/g}$ FW) in leaves, roots, and shells, but very little (0.05-0.06 $\mu\text{g/g}$ FW) was found in developing seeds and seed coats of field-grown peanuts. Accumulation of resveratrol in leaves increased over 200-fold in response to UV light, over 20-fold in response to paraquat, and between 2- and 9-fold in response to wounding, H_2O_2 , salicylic acid (SA), jasmonic acid, and ethephon, 24 h after treatment. Changes in resveratrol content were correlated with levels of resveratrol synthase (RS) mRNA, indicating a transcriptional control of resveratrol synthase activity [40]. These gene changes underline the biochemical and physiological changes induced by UV-C such as increased defense ability, delayed softening, better maintenance of nutritional and sensory qualities and extension of shelf-life [30-31]. Table 2 summarizes the changes in phytoalexin content with postharvest UV-C treatment of some crops.

Crop	UV-C conditions	Results	Source
Tomato (cv. Zhenfen 202)	4.0 kJm^{-2} and storage at 14°C for 24 h	A number of PR genes, like PR5-like protein, β -1,3-glucanase and chitinase were highly up-regulated in response to UV-C treatment.	[31]
Peanut Seedlings	300 μWcm^{-2} at 15 cm for 1 h and storage at 25°C for 60 h	Resveratrol concentrations increased immediately after UV-C radiation and peaked at 12 h, followed by a decline nearly to control concentrations by 24 h, indicating that resveratrol synthesis could be induced by UV-C irradiation.	[38]
Star Ruby grapefruit	0.5 kJm^{-2} , 1.5 kJm^{-2} , and 3.0 kJm^{-2} and storage at 7°C for 28 days	Scoparone and scopoletin increased in flavedo tissue with UV treatment. Both phytoalexins showed similar accumulation patterns, although the concentrations of scoparone were much lower than those of scopoletin and when compared to non-irradiated fruit that exhibited no detectable levels of scoparone and scopoletin.	[41]
Tomato	3.7 kJm^{-2} and storage at 7°C for 35 days	UV-C dose induced synthesis and accumulation of rishitin. The capacity to accumulate rishitin declined with ripening in both control and UV-treated fruit.	[42]

Table 2. Summary of changes in phytoalexin content with postharvest UV-C treatment of crops.

5.2.2. Phenolics and flavonoids

The largest category of phytochemicals and most widely distributed secondary products in plants are the phenolics. They exist in higher plants in many different forms including hydroxybenzoic derivatives, cinnamates, flavonoids (flavonols, flavones, flavanols, flavanones, isoflavones, proanthocyanidins), lignans, and stilbenes, and affect quality characteristics of plants such as appearance, flavor, and health-promoting properties. Besides their role as antioxidants, phenolic compounds also possess antimicrobial properties and are involved in disease resistance by contributing to the healing of wounds by lignification of cell walls around wounded sites [44]. The accumulation of phenolic and flavonoid compounds may act as a protective filter against excessive UV radiation [28, 45-48]. Phenolics also serve as substrates for browning reactions. The enzymes phenylalanine ammonia-lyase (PAL; EC 4.3.1.5), polyphenol oxidases (PPO; EC 1.14.18.1) and peroxidases (POD; EC 1.11.1.7) are the main enzymes responsible for phenolic degradation that often leads to quality loss in crops [44]. Skin discoloration or external browning is one effect of UV-C treatment and is dose dependent with the effect being more pronounced as the dose is increased and has been reported in several crops notably tomato, strawberries, peaches, and Star Ruby grapefruit [28]. Table 3 summarizes the changes in Phenolics content with postharvest UV-C treatment of some crops. Time course measurements of the effects of UV-C have shown that the strongest responses of fruit to UV-C treatment occurred instantly after the illumination and the effects diminished with time.

Crop	UV-C conditions	Results	Source
<i>Spilanthes acmella</i> (toothache plant)	1.5 kJm ⁻² and storage in field conditions after 3 and 5 days	Anthocyanin and flavonoid concentration increased with UV-C treatment.	[29]
Banana (cv. Cavendish)	0.02 kJm ⁻² , 0.03 kJm ⁻² , UV-C doses reduced both the incidence of CI and its severity and 0.04 kJm ⁻² and storage at 5 and 25°C for 7 and 21 days	activated PAL and resulted in higher levels of total phenolic compounds in comparison with untreated controls.	[30]
Yellow Bell Pepper	2.2 kJm ⁻² , 4.4 kJm ⁻² , and 6.6 kJm ⁻² and storage at 12 ± 1°C for 15 days	UV-C illumination at 6.6 kJ/m ² enhanced total flavonoid content.	[32]
Pear (cv. Yali)	5 kJm ⁻² and storage at 20°C for 42 days	Enzyme activities of PAL and β-1,3-glucanase were induced to high levels by UV-C treated pears and thought to be responsible for the reduction in postharvest decay.	[33]
Tomato (cv. Capello)	3.7 kJm ⁻² and 24.4 kJm ⁻² and storage at 16°C for 28 days	A 4.5- and 4.9-fold increase in total phenols with UV doses of 3.7 kJm ⁻² and 24.4 kJm ⁻² , respectively, when compared to controls on day 14 was observed. Levels of total phenols were higher with UV-treated fruits than controls at the end of the storage.	[36]

Crop	UV-C conditions	Results	Source
<i>Turnera diffusa</i> Willd (<i>Damiana</i> medicinal plant)	0.38 mWcm ⁻² ; 5, 10 min day ⁻¹ and 20 min day ⁻¹ exposure and storage for 10 days	Levels of phenols increased immediately upon exposure to UV-C dose (5 min day ⁻¹) and in all UV-C doses (5, 10 and 20 min day ⁻¹) by day 7.	[37]
Tomato (Light Red and Mature Green)	1.0 kJm ⁻² , 3.0 kJm ⁻² , and 12.2 kJm ⁻² and storage at RT for 2 days	UV-C doses (3.0 kJm ⁻² and 12.2 kJm ⁻²) caused a 1.2-fold increase in total phenolics of both maturities but the same effect was not observed in the individually analyzed phenolic compounds.	[45-46]
Fresh-cut pineapple (cv. Honey), banana (cv. Pisang mas) and Thai seedless guava	10 min day ⁻¹ , 20 min day ⁻¹ , and 30 min day ⁻¹ exposure and storage at RT	In bananas and guava, UV-C radiation resulted in an increase in total phenols and flavonoids. In pineapples however, there was a significant increase in flavonoids but UV-C irradiation did not have any significant increase in total phenol content.	[47]
Fresh-cut Mango (cv. Tommy Atkins)	1 min day ⁻¹ , 3 min day ⁻¹ , 5 min day ⁻¹ , and 10 min day ⁻¹ exposure and storage at 5°C for 15 days	An increase in the total phenols and total flavonoids were observed for all doses, with the longer irradiation exposure time proportional to the increases in levels of total phenols and flavonoids and lowest antioxidant capacity with controls.	[48]
Blueberries	0.43 kJm ⁻² , 2.15 kJm ⁻² , 4.30 kJm ⁻² , and 6.45 kJm ⁻² and held for various times at 20°C	UV-C doses increased total phenols and anthocyanins levels versus controls. Levels of flavonoids in blueberries increased with UV-C doses. Significantly higher antioxidant capacity in blueberries was detected in fruit treated with doses of 2.15 kJm ⁻² and 4.30 kJm ⁻² compared to the control fruit.	[49]
Button mushrooms	0.225 kJm ⁻² , 0.45 kJm ⁻² , and 0.90 kJm ⁻² and storage at 4°C for 21 days	Although there was a general increase in total phenolics during storage, UV doses showed lower total phenolics content during the first week of storage beyond which there was no significant difference among treatments.	[50]
Korla Pears	3 kJm ⁻² and 6 kJm ⁻² and storage at 20°C for 15 days	UV-C 3 kJm ⁻² dose had higher levels of total phenolics compared to the dose of 6 kJm ⁻² and control. Similar results were noted for flavonoids where at the end of storage, residual flavonoid content in control was 82% of initial values compared with 108% in 3 kJm ⁻² dose, and 98% in 6 kJm ⁻² dose of initial values.	[51]
Broccoli heads (cv. de Cicco)	4 kJm ⁻² , 7 kJm ⁻² , 10 kJm ⁻² , or 14 kJm ⁻² and storage at 20°C for 6 days	Total phenols and flavonoids increased in both control and UV-treated broccoli. Lower levels of total phenols and flavonoids were found in UV-treated florets after 4 and 6 days in storage compared to controls.	[53]

Table 3. Summary of changes in phenolics and flavonoids content with postharvest UV-C treatment of crops.

5.2.3. Photosynthetic pigments, antioxidants carotenoids, lycopene and vitamins α -tocopherol and ascorbic acid

5.2.3.1. Chlorophyll

During chlorophyll degradation, chlorophyll *a* is transformed to chlorophyllide *a* through the action of the chlorophyllase enzyme [52]. Chlorophyllide *a* is then acted by the enzyme Mg-dechelatase removing Mg^{2+} from the molecule and forming pheophorbide *a*, consequently the green color is lost. In general, the chloroplast is the first organelle to show injury response with UV radiation and reduction in the chlorophyll contents may be due to inhibition of biosynthesis or due to degradation of chlorophyll and their precursors [29]. Table 4 summarizes the changes in chlorophyll content with postharvest UV-C treatment of some crops. Photosynthetic pigments such as chlorophyll *a* and *b* as well as total chlorophyll contents were considerably reduced in UV-C treated crops [29, 37]. In these studies, chlorophyll *a* and chlorophyll *b* were more sensitive to UV-C radiation. The reduction of chlorophyll content is thought to have a negative effect on plant photosynthetic efficiency due to UV-C radiation being too severe. Previous studies have demonstrated the inhibitory effect of UV-C light on chlorophyll breakdown and on the activities of Mg-dechelatase, chlorophyllase and chlorophyll degrading peroxidase in crops [53-55].

Crop	UV-C conditions	Results	Source
<i>Spilanthes acmella</i> (toothache plant)	1.5 kJm^{-2} and storage in field conditions after 3 and 5 days	Chlorophyll <i>a</i> , chlorophyll <i>b</i> , and total chlorophyll contents were considerably reduced with UV-C treatment.	[29]
<i>Turnera diffusa</i> Willd (Damiana medicinal plant)	0.38 mWcm^{-2} ; 5 min day^{-1} , 10 min day^{-1} , and 20 min day^{-1} exposure and storage for 10 days	Chlorophyll <i>a</i> content significantly decreased in plants exposed to UV-C radiation for 5 and 20 min day^{-1} while chlorophyll <i>b</i> content significantly decreased with UV-C 20 min day^{-1} dose relative to control plants.	[37]
Broccoli heads (cv. de Cicco)	4 kJm^{-2} , 7 kJm^{-2} , 10 kJm^{-2} , or 14 kJm^{-2} and storage at 20°C for 6 days	All UV treatments delayed yellowing and chlorophyll degradation. UV-C dose of 10 kJm^{-2} reduced the degradation of both chlorophyll <i>a</i> and <i>b</i> in broccoli florets and this was correlated to a reduced activity of chlorophyllase and chlorophyll peroxidase in treated florets, which maintained a greener color than the controls. UV-C treated broccoli also maintained lower Mg-dechelatase level than controls.	[53]
<i>Brassica oleracea</i> var. <i>alboglabra</i> (Chinese kale)	1.8 kJm^{-2} , 3.6 kJm^{-2} , 5.4 kJm^{-2} , and 7.2 kJm^{-2} and storage at 20°C for 8 days	UV-C doses of 3.6 kJm^{-2} and 5.4 kJm^{-2} delayed leaf yellowing and chlorophyll loss depicted as higher chlorophyll contents and lower activity of chlorophyllase, Mg-dechelatase and chlorophyll-degrading peroxidase as compared to the other treatments.	[54]

Crop	UV-C conditions	Results	Source
Mature Green Tomato (cv. Capello)	3.7 kJm ⁻² and 24.4 kJm ⁻² and storage at 16°C for 28-35 days	There was a significant decrease in chlorophyll degradation, with levels significantly higher in UV-C treated fruit compared to controls with storage time for both UV-C doses.	[55]

Table 4. Summary of changes in chlorophyll content with postharvest UV-C treatment of crops.

5.2.3.2. Carotenoids and lycopene

Carotenoids (β -carotene) or pro-vitamin A are quenching agents that facilitate the return of singlet oxygen to its ground state. Table 5 summarizes changes in Total Carotenoids Content (TCC) and Lycopene content with postharvest UV-C treatment of some crops. In some cases, decreases in β -carotene as a result of UV-C treatment, are due most likely to the phenomenon of photobleaching [37, 45]. These observations appear to be at variance with those of other authors where carotenoid levels increased in medicinal plants [29], tomato [55], and minimally processed carrots [61] with UV-C treatment. The increase in total carotenoids may be part of the antioxidant system where carotenes are involved in protection of the chloroplast against photooxidation.

Crop	UV-C conditions	Results	Source
<i>Spilanthes acmella</i> (toothache plant)	1.5 kJm ⁻² and storage in field conditions after 3 and 5 days	TCC increased with UV-C treatment. Lycopene was not analyzed.	[29]
Yellow Bell Pepper	2.2 kJm ⁻² , 4.4 kJm ⁻² , and 6.6 kJm ⁻² and storage at 12 ± 1°C for 15 days	UV-C illumination at 6.6 kJ/m ² enhanced TCC.	[32]
<i>Turnera diffusa</i> Willd (<i>Damiana</i> medicinal plant)	0.38 mWcm ⁻² ; 5 min day ⁻¹ , 10 min day ⁻¹ , and 20 min day ⁻¹ exposure and storage for 10 days	TCC significantly decreased in plants exposed to UV-C (20 min day ⁻¹) compared to control. Lycopene was not analyzed.	[37]
Light Vine-Ripe Red Tomato	1 kJm ⁻² , 3 kJm ⁻² , and 12.2 kJm ⁻² and storage at RT for 2 days	UV-C doses caused a decrease in β -carotene while UV-C doses at 1 kJm ⁻² and 12.2 kJm ⁻² enhanced the increase in total lycopene (<i>E</i> + <i>Z</i> isomers), by about 20% over control samples. UV-C 1 h treatment favored an increase in <i>E</i> -lycopene, while UV-C 12 h treatment affected mainly <i>Z</i> -isomers, which is considered to be better from a nutritional point.	[45]
Mature Green (Breaker stage) Tomato	1 kJm ⁻² , 3 kJm ⁻² , and 12.2 kJm ⁻² and	UV-C doses caused a decrease in β -carotene while total lycopene increased 8-fold at doses of 1.0 kJm ⁻² and 3.0 kJ/m ²	[46]

Crop	UV-C conditions	Results	Source
	storage at RT for 8 days	over those of control. <i>E</i> -lycopene decreased with 12.2 kJ/m ² dose.	
Fresh-cut Mango (cv. Tommy Atkins)	1 min day ⁻¹ , 3 min day ⁻¹ , 5 min day ⁻¹ , and 10 min day ⁻¹ exposure and storage at 5°C for 15 days	β -carotene content decreased with storage in all treatments including controls with the major reduction observed in fruits treated for 10 mins and 5 mins. [48]	
Mature Green Tomato (cv. Capello)	3.7 kJm ⁻² and 24.4 kJm ⁻² and storage at 16°C for 28-35 days	There was a significant decline in lycopene accumulation with time for both UV-doses. UV-3.7 kJm ⁻² exhibited significantly higher levels of TCC compared to control fruits throughout storage. [55]	
Mature Green (Breaker stage) Tomato	13.7 kJm ⁻² and storage at 12°C-14°C for 21 days	Lycopene content was enhanced by UV-C treatment but the concentration of β -carotene was not affected by UV-C. [56]	
Mature Green Tomato	3.7 kJm ⁻² and storage at 13°C for 30 days	UV treatment significantly reduced the lycopene content. [57]	
Fresh-cut Carrots (cv. Nantes)	0.78-0.36 kJm ⁻² and storage at 5°C for 10 days	A 64% loss in TCC in UV-C treated samples compared to controls was noted just after processing. However, UV samples exhibited a consistent increase in TCC levels with levels reaching 3-fold higher at day 7 than at day 0. [61]	

Table 5. Summary of changes in total carotenoids content (TCC) and lycopene with postharvest UV-C treatment of crops.

5.2.3.3. α -tocopherol (Vitamin E)

Alpha-tocopherol is a major lipid-soluble antioxidant that breaks the chain of free radical reactions of polyunsaturated fatty acids (PUFAs) in cell membranes. Alpha-tocopherol protects membrane PUFAs from ROS and free radical damage by reacting with lipid radicals produced in the lipid peroxidation chain reaction [16]. Levels of tocopherol in plants are as a result of synthesis, recycling, and degradation. Changes in α -tocopherol levels during plant responses to environmental stress are characterized by two phases; in the first phase there is an increase in tocopherol synthesis that was followed by a second phase of net tocopherol loss [24]. Endogenous α -tocopherol levels are also severely affected by the extent of its degradation and recycling under stress. As stress is more severe and the amounts of ROS in chloroplasts increase, α -tocopherol levels tend to decrease. Irreversible degradation of α -tocopherol may also occur when α -tocopheroxyl radicals, which result from the scavenging of lipid peroxy radical by α -tocopherol, are not recycled back by ascorbate. Table 6 summarizes the changes

in α -Tocopherol (Vitamin E) content with postharvest UV-C treatment of some crops. While it has been reported that α -tocopherol levels increase in photosynthetic plant tissues in response to a variety of abiotic stresses, results from a study with UV-C irradiated tomato exocarp demonstrated declining levels and do not support the hypothesis that antioxidants such as α -tocopherol are stimulated for plant defense against oxidative stress caused by UV-C radiation [36]. On the other hand, the increased vitamin E content in medicinal *Damiana* plants exposed to UV-C radiation may provide protection against the oxidative damage induced by UV-C radiation [37].

Crop	UV-C conditions	Results	Source
Tomato (cv. Capello)	3.7 kJm ⁻² and 24.4 kJm ⁻² and storage at 16°C for 28 days	Levels of α -tocopherol were considerably lowered with UV treatment.	[36]
<i>Turnera diffusa</i> Willd (Damiana medicinal plant)	0.38 mWcm ⁻² ; 5 min day ⁻¹ , 10 min day ⁻¹ , and 20 min day ⁻¹ exposure and storage for 10 days	Levels of α -tocopherol increased with UV treatment.	[37]

Table 6. Summary of changes in α -Tocopherol (vitamin E) content with postharvest UV-C treatment of crops.

5.2.3.4. Ascorbic acid (Vitamin C)

Vitamin C content, considered to be a nutritional quality index for fruits and vegetables occurs as L-ascorbic acid and dehydroascorbic acid (oxidised form of ascorbic acid). Ascorbate is an electron donor and this property explains its function as an antioxidant or reducing agent and is easily destroyed by oxidation, exposure to light or high temperatures. Ascorbic acid scavenges free radicals in the water soluble compartment of the cell and may also regenerate α -tocopherol (vitamin E), an important lipid-phase antioxidant [16]. Table 7 summarizes the changes in ascorbic acid (vitamin C) content with postharvest UV-C treatment of some crops. In most cases, UV-C treatment decreased the vitamin C content of fruits or did not affect ascorbic acid levels.

Crop	UV-C conditions	Results	Source
Yellow Bell Pepper	2.2 kJm ⁻² , 4.4 kJm ⁻² , and 6.6 kJm ⁻² and storage at 12 ± 1°C for 15 days	No effect on ascorbic acid levels with UV-C treatment.	[32]
Tomato (cv. Capello)	3.7 kJm ⁻² and 24.4 kJm ⁻² and storage at 16°C for 28 days	UV treatment decreased ascorbic acid levels.	[36]

Crop	UV-C conditions	Results	Source
Fresh-cut pineapple (cv. Honey), banana (cv. Pisang mas) and Thai seedless guava	10 min day ⁻¹ , 20 min day ⁻¹ , and 30 min day ⁻¹ exposure and storage at RT	UV treatment decreased ascorbic acid levels.	[47]
Fresh-cut Mango (cv. Tommy Atkins)	1 min day ⁻¹ , 3 min day ⁻¹ , 5 min day ⁻¹ , and 10 min day ⁻¹ exposure and storage fruits irradiated for 10 min. at 5°C for 15 days	A reduction in total ascorbic acid content with UV treatment was observed. The lowest values for ascorbic acid occurred in	[48]
Button mushrooms	0.225 kJm ⁻² , 0.45 kJm ⁻² , and 0.90 kJm ⁻² and storage at 4°C for 21 days	Apart from day 1 where UV treated mushrooms had lower ascorbic acid content than controls, during storage, levels increased to a maximum at day 14 and remained stable until day 21 for both control and UV-treated mushrooms.	[50]
Tomato (cv. Trust)	3.7 kJm ⁻² at and storage at 16°C for 25 days	Ascorbate oxidase activity exhibited a decline during storage for both control and UV-C treated fruit, however the amount of this enzyme was lower in UV-C-treated fruit and could correlate to decreases in levels of ascorbic acid.	[58]
Fresh-cut mature green bell pepper	3 kJm ⁻² , 10 kJm ⁻² , and 20 kJm ⁻² and storage at 10°C for 8 days	The antioxidant capacity of UV-C-treated fruit did not change during storage, but showed a slight increase in the control.	[59]
Fresh fruit juices	Various time intervals of exposure to UV-C	UV treatment decreased ascorbic acid levels. The longer the exposure to UV, the higher the losses of ascorbic acid content in fruit juices.	[60]

Table 7. Summary of changes in ascorbic acid (vitamin C) content with postharvest UV-C treatment of crops.

5.2.4. Glutathione

Thiol (-SH) groups and other functions readily donate hydrogen atoms and are scavengers of hydroxyl radicals. The tri-peptide Glutathione (γ -glutamylcysteinylglycine) is a major free non-protein thiol compound found in plant tissues. In non-stressed cells, 90% of glutathione is mainly present in its reduced form (GSH) while the oxidized GSSG levels are lower. Upon oxidative stress, the glutathione redox status may shift to a more oxidized form, $\text{ROOH} + 2\text{GSH} \rightarrow \text{ROH} + \text{GSSG} + \text{H}_2\text{O}$, due to increased GSH oxidation and/or decreased GSSG reduction. Such a shift in the glutathione status in plants has been reported upon exposure to a variety of environmental factors associated with oxidative stresses [62]. The ratio of reduced GSH to oxidized GSSG within the cells can be used to measure cellular toxicity. Table 8 summarizes the changes in glutathione content with postharvest UV-C treatment of some crops. Although glutathione has been used as an oxidative stress indicator in plants, there is conflicting evidence about glutathione responses under oxidative stress conditions. While some studies have found an increase in glutathione synthesis in response to oxidative stress, others have found no increase in GSH by environmental stresses.

Crop	UV-C conditions	Results	Source
Strawberry	0.43 kJm ⁻² , 2.15 kJm ⁻² , and 4.3 kJm ⁻² and storage at 10°C for 15 days	UV-C enhanced the increase of GSH in strawberry fruit during storage.	[34]
Tomato (cv. Capello)	3.7 kJm ⁻² and 24.4 kJm ⁻² and storage at 16°C for 28 days	UV-C treatment did not enhance GSH levels when compared to non-irradiated fruit.	[36]
Young Pea Plants	9 kJm ⁻² and storage up to 72 h	Apart from the initial increase in free thiols by 20% with UV-C, free thiol levels decreased with UV-treatment.	[63]

Table 8. Summary of changes in glutathione content with postharvest UV-C treatment of crops

5.2.5. Polyamines(PAs)

Polyamines (PAs) are implicated in a variety of regulatory processes ranging from regulation of growth and cell division, regulating the activity of ribonucleotides and proteinase to inhibition of ethylene (C₂H₄) production and senescence. The anti-senescent activity of PAs may also be related to their ability to be effective free radical scavengers, as well as stabilizing DNA and membranes by their positively charged cations associating with negative charges on nucleic acids and phospholipids [26]. Changes in plant PA metabolism occur in response to a variety of abiotic stresses and have been shown to enhance the ability of plants to resist environmental stresses. However, the physiological significance of elevated PA levels in abiotic stress responses is still unclear in terms of whether such a response is as a result of stress-induced injury or a protective response to abiotic stress [64]. Table 9 summarizes the changes in PA content with postharvest UV-C treatment of some crops.

Crop	UV-C conditions	Results	Source
Young Pea Plants	9 kJm ⁻² and storage up to 72 h	Exogenous application of PA (spermine) plus UV-C positively affected the plant in maintaining normal plant growth, stabilizing cell membranes and activating non-enzymatic antioxidants.	[63]
Tomato (cv Capello)	3.7 kJm ⁻² and 24.4 kJm ⁻² and storage at 16°C for 21 days	UV-C treatment induced PA (free Putrescine) accumulation in tomato fruit. By day 21, levels were still high in UV-treated fruit compared to controls. Similarly, in another recent study, PA content of UV-C (3.7 kJm ⁻²) treated tomato were higher than controls.	[65-66]
Strawberry	0.72 kJm ⁻² and storage at 4°C	Exogenous application of 2 mM putrescine plus UV-C resulted in positive effects on maintenance of firmness, reduction of weight loss and protection of total antioxidant capacity and vitamin C content against degradation.	[67]

Crop	UV-C conditions	Results	Source
Intact Pea Plants	0.1 kJm ⁻² and 0.3 kJm ⁻² and storage	Endogenous free, conjugated, and bound PAs (Spm, Spd, and Put) in leaves of young pea plants reduced membrane damage as a result of UV-C irradiation.	[68]

Table 9. Summary of changes in polyamine (PA) content with postharvest UV-C treatment of crops.

6. Conclusions

Studies on the benefit of phytochemicals continue to be of interest, as researchers have been exploring alternative medicine in the management of common lifestyle diseases and preventative actions, as well as the promotion of good health and nutrition. Abiotic stresses are significant determinants of quality and nutritional value of crops during their life cycle. Notwithstanding, climate change has created additional environmental variables that may influence postharvest stress susceptibility of crops. While breeding programs are underway for many crops to develop stress resistance that will allow them to adapt to climate change, it is not clear that breeding for stress resistance in the field will also extend to stress resistance characteristics of harvested crops particularly fresh fruits and vegetables and fresh-cut produce. Proper postharvest management of crops can positively influence susceptibility to abiotic stress. It is important to understand the various response networks to abiotic stresses encountered in the field and in the postharvest continuum to better evaluate the benefits that may yield from such stresses. Controlled stresses may be used as tools by the fresh produce and food processing industries to obtain enhanced phytochemical or health promoting components of fresh-cut or whole fresh produce and for growers interested in finding alternative uses for their crops. In the context of the different postharvest handling treatments, the potential of UV-C irradiation has enormous possibilities as a non-chemical treatment to sanitize and reduce microbial loads, delay ripening, and improve shelf-life of fresh fruits and vegetables. Further, the elicitation of health promoting phytochemicals with UV-C is an indication that such an approach may be of benefit to growers, processors, and consumers in enhancing sensory characteristics of fresh fruits and vegetables. The beneficial action of UV-C is thought to be as a result of the activation of multiple defense systems involving secondary stress metabolites such as phytoalexins and enzymic and non-enzymic antioxidants. The intensification of natural defense mechanisms of higher plant so that they can defend themselves against infection or adverse stresses is one alternative approach to controlling post-harvest losses. Depending on the experimental conditions including UV-C dose, commodity, maturity stage, storage, and environmental conditions administered, such bioactive compounds have been found to be variable, in some instances may decrease or increase, and this change may impact quality of the crops. In many studies, the strongest responses to UV-C treatment occurred almost immediately after the illumination with some beneficial effects of crops occurring after UV-C treatment with the effects decreasing with time. There is need for further research on the molecular and biochemical mechanisms by which these beneficial responses are derived in UV-C treated fresh fruits and vegetables. This is in order to help guide the development of approaches to reliably confer health and nutritional benefits. The potential

application of UV-C is novel and relevant particularly for the fresh fruit and vegetable and fresh-cut trade industries.

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