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Gaseous ozone in postharvest storage: Mechanisms, efficacy and limitations

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ABSTRACT

The use of gaseous ozone as postharvest treatment of fruit and vegetables is described and discussed with the aim of critically analyse main mechanisms involved in the production, degradation and interaction with horticultural products during storage. By particularly focusing on the effects on fruit ripening delaying and metabolic changes, the analysis of literature was conducted with the aim of highlighting the state of the art, contradictory aspects, and further directions to be taken into considerations for a reliable scalability of the technology. Ozone oxidative interactions are complex and are a function of numerous variables related to operative parameters and product characteristics. A critical analysis of these aspects appears mandatory for the definition of useful operative guidelines aimed at avoiding losses and preserving, at the same time, nutritional and organoleptic attributes of fruits and vegetables.

1. Introduction

The quality of a fruit is a major driver in consumer preference and market potentiality and are generated and established as result of a series of physiological processes occurring during ripening. Although originally evolved to promote the dispersion of seeds, these modifications also render the fruit more appealing and palatable. Since the ripening modifications interest a diverse numbers of physiological processes, they have to be uniformly coordinated by endogenous hormones (Gapper et al., 2013; Giovannoni, 2001; Zenoni et al., 2023). Fruit ripening is however the last step before senescence, therefore, the continuous progression of the events making the fruit suitable for consumptions, also lead to fruit decay, primarily associated to an important and irreversible dismantling of the cell wall. To prevent fruit wastage while promoting the availability of fresh fruit on the market, several postharvest technologies have been applied to interfere with ethylene, effectively delaying the ripening progressions and softening. In addition to refrigeration, controlled atmosphere and the exogenous application of ethylene inhibitor (AVG: aminoethoxyvinylglycine) or ethylene competitor (1-MCP: 1-methylcyclopropene) have been applied to control the fruit ripening progression (Hoffmann et al., 2025). Although these are standard technologies regularly applied, novel strategies are needed, to make the fruit storage more efficient and sustainable.

During the last ten years, there has been a significant increasing interest in the use of ozone, in aqueous or gaseous phase, as a postharvest treatment of fruit and vegetables aiming at reducing microbial contamination and at extending the shelf-life during storage, by preserving, at the same time, attributes related to sensorial and nutritional quality. Ozone gas has been explored either as a one shot pre-storage treatment or as a continuous or intermittent storage tool (Sitoe et al., 2025). Current data about the interaction between ozone and horticultural products is sometimes contradictory and many aspects still remain to be fully clarified, particularly those related to reliable mechanisms involved in the decomposition steps especially in real postharvest storage. These topics are extremely relevant for the final fruit marketability. Moreover, while ozone is largely applied to control the development of pathogen or biotic agents, its role in controlling ethylene metabolism and ripening progression is not yet comprehensively investigated.

At atmospheric pressure, O_3 is normally generated through electrical non-equilibrium discharges and quickly starts to decompose according to temperature, humidity and air speed (McClurkin & Maier, 2010) and to the type of molecules present in the storage room atmosphere (Cullen et al., 2009). In turn, ozone interacts with vegetable cells, and entering the product through natural openings establish both direct (ozone) or

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indirect (free oxygen radicals) oxidative reactions (Loreto & Fares, 2007; Sitoe et al., 2025). However, the predominance of the oxidative reaction type is not fully discussed, especially considering the real postharvest operative conditions, the superficial characteristics of horticultural products, the presence of microorganisms (type and load), and the possible penetration ability of the gas.

This review aims at providing a new and comprehensive analysis of the ozone-horticultural products interaction during postharvest storage, with a specific focus on its possible role on ripening dynamics and metabolism. Starting from a summary of the state of the art of the research conducted on these topics, both in terms of proposed mechanisms and postharvest applications, the present review offers a survey of the main realistic oxidative mechanisms, the biochemical effects, the stimulation of defence mechanisms and practical implications related to the use of ozone as postharvest strategy. Potential strategies and further directions for the improvement of the product shelf life through ozone gas treatments in postharvest facilities will be also highlighted and discussed.

2. Ozone gas: mechanisms of generation and decomposition

Ozone gas can be efficiently generated through electrical discharges produced by flowing both air and oxygen through dielectric barrier discharges (DBD), as first introduced by Siemens (1857).

DBD, better known as atmospheric non-equilibrium or silent discharges, occur between two metal electrodes separated by a few millimetre small gap with the presence of one or more dielectric layers in the discharge space. By using these configurations, the non-equilibrium conditions can be obtained according to different geometric arrangements, gas medium types and operative parameters. Generally, low loss dielectrics characterised by high breakdown strength (mainly glass, quartz or ceramic) are used to limit the current flow and ensure a uniform discharge distribution (Kogelschatz et al., 1997). Common DBD electrodes configurations can be characterised by planar (the electrodes are parallel) or cylindrical (the electrodes are arranged in a coaxial manner) as illustrated in Fig. 1 and operate with alternating driving high voltages (1–100 kV) in the 500 Hz-500 kHz frequency range (Nehra et al., 2008).

Operatively, at atmospheric pressure and by considering most gases, a large number of short lived (nanosecond duration) microdischarges are formed and statistically distributed across the gap according to a non-thermal plasma process (NTP). These microdischarges are current filaments, 100 μm radius cylindrical channels spreading, at the dielectric surface, into a bigger surface discharge. As known, the strength of these microdischarges influences the efficiency of the ozone production whereby factors as configuration and gap spacing, gas pressure, type of dielectric and electrodes metals, can play the main role in the DBD patterns (Kogelschatz et al., 1988). The main mechanism of ozone generation in dielectric barrier discharges, taking place in the above described microdischarge channels, is a well-established two-step process and mainly refers to the work conducted by Kogelschatz et al. (1988) and Eliasson et al. (1987). Accordingly, by considering pure oxygen gas feeding, the cited process starts by the excitation and dissociation of O_2 molecules induced by electrons (e^-):

$$e^- + O_2 \rightarrow e + O_2\left(A^3\sum\nolimits_u +\right) \rightarrow e + O(^3P) + O(^3P) \tag{1}$$

$$e + O_2 \rightarrow e + O_2\left(B^3\sum\nolimits_u -\right) \rightarrow e + O(^3P) + O(^1D) \tag{2}$$

with the two electronic dissociation processes characterised by 6 eV ($A^3\Sigma_{u,}^+$ first electronically excited triplets of the oxygen molecule) and 8.4 eV ($B^3\Sigma_u^-$, the second excited triplet Sigma state of oxygen molecule) energy thresholds, respectively. Starting from oxygen atoms, ozone is then formed through a three-body collision reaction:

$$O + O_2 + M \rightarrow O_3^* + M \rightarrow O_3 + M \tag{3}$$

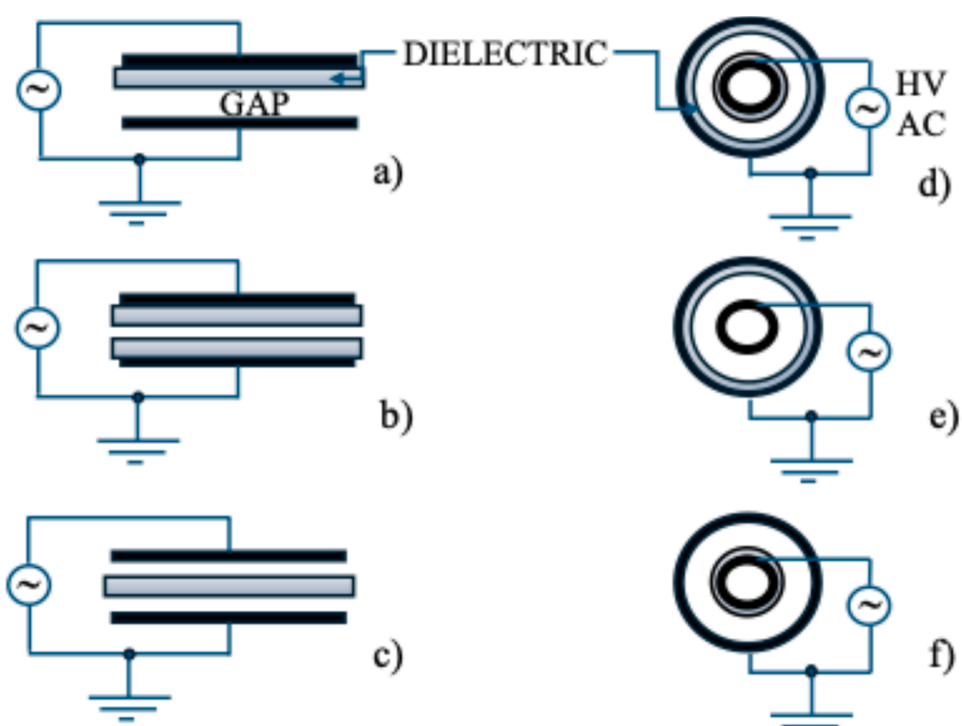

Fig. 1. Dielectric Barrier Discharge (DBD) configurations.
Planar electrode arrangements (a, one dielectric barrier on the powered electrode; b, two dielectric barriers on both electrodes; c, dielectric barrier between the two electrodes). Cylindrical electrode arrangements (d, two dielectric barriers on both electrodes; e, dielectric barrier on the inner side of the other electrode; f, dielectric barrier between the electrodes).

where M is a neutral collision species (O, O_2, O_3 or N_2 for air) accepting the extra electron energy and where O_3* is an excited transient ozone species.

In the microdischarge channels, the generation and the decomposition of O_3 can be considered a simultaneous process and, in terms of competitive reactions, the following paths can play the main role (Kogelschatz et al., 1997):

$$e + O_3 \rightarrow e + O_2 + O \quad (4)$$

$$O_3^* + O \rightarrow O_2 + O_2 \quad (5)$$

$$O_3 + O \rightarrow O_2 + O_2 \quad (6)$$

Respect to pure oxygen gas, ozone generation in air increases in complexity because of the formation of excited and dissociated forms of nitrogen molecules along with ionic specie as N^+ and N_2^+. Even though oxygen atoms can be generated also through the reaction between O_2 and excited nitrogen molecules, the ozone production efficiency is reduced compared to oxygen feeding, because of the "parasitic" formation of nitrogen oxides (NO_x), which can catalyse ozone decomposition (Chonpan et al., 2025):

$$NO + O_3 \rightarrow NO_2 + O_2 \quad (7)$$

$$NO_2 + O \rightarrow NO + O_2 \quad (8)$$

By focusing on the volumetric concentration of the produced ozone as a function of the operating conditions of the DBD system, it resulted that for O_3 generation with both oxygen gas and dry air, the optimal operating conditions is obtained with the lower flow rates and by feeding oxygen gas instead of dry air (Yehia, 2015).

Ozone, once formed from the microdischarge channels, can diffuse and diluted into the surrounding gas. In addition, the O_3 gas initiates to decompose as a function of temperature, relative humidity, air movement, types of surfaces and organic or inorganic matter. In general, by increasing temperature, relative humidity and air speed, a decrease of the time required to half the ozone concentration ($t_{1/2}$) is observed. The gas rapidly decomposes as a consequence of the interaction with surfaces, mainly with unsaturated carbon-carbon bonds as natural rubbers and neoprene and unsaturated organic compounds adsorbed on indoor surfaces. These possible interactions could reduce the O_3 concentration with a consequent negative effect on the target oxidation mechanisms, generating, at the same time, harmful by-products such as aldehydes and ketones (Weschler, 2000).

Indoor volatile organic compounds (VOCs) and inorganic gases could also play a significant role in the O_3 decomposition kinetics. On the basis of common indoor VOCs and inorganic gases proposed by Weschler (2000) (Weschler, 2000), although details about atmospheric conditions were not reported, $t_{1/2}$ values of 4.1 days (Ethylene), 0.57 days (Isobutene) and 0.0004 days (Nitric Oxide) were described. As reported by literature, the ozone gas decomposition kinetics in the air space can be increased with organic materials, such as agricultural products. The related microbial, chemical and physical properties in addition to temperature and the moisture content can play a relevant role (Alencar et al., 2011; De Oliveira et al., 2020). Clarifying all main reaction and decomposition kinetics is mandatory when this technology is employed in industrial horticultural post-harvest storage solutions, especially for the definition of the most appropriate O_3 concentrations and times of exposures, to maximise treatment efficacy avoiding possible negative effects on the quality of the produce.

The possible role of the medium in the gaseous ozone half-life time should be explored also in terms of type and load of microorganisms adhering to the surface of the horticultural products. Differently from experiences coming from aqueous systems, literature is absent on this topic, clearly related to the different mechanisms of induced oxidation.

3. Mechanisms of ozone induced oxidation

Ozone can oxidize a large amount of organic and inorganic substances. Two main oxidative mechanisms are reported for the interaction between ozone and agri-food products. The first mechanism is related to the direct ozone oxidation of target organic compounds, while the second, whose role in the gaseous phase will be discussed, involves the generation of free oxygen radicals from indirect mechanisms (Cullen et al., 2009). Ethylene and wall-modifying enzymes expressed during ripening can be considered main O_3 target molecules involved in post-harvest ripening and metabolism alterations. In addition, all main biopolymers characterising cuticle, cell membranes and wall architecture, particularly phospholipids, cellulose and hemicellulose and pectin could be negatively affected by the interaction with ozone.

3.1. Direct oxidative mechanisms

Direct oxidative mechanisms take place because of the capability of ozone to directly act as an oxidant species in electron transfer reactions. By considering reactivity of molecules characterising both the environmental gas phase and the horticultural matter, electrophilic and nucleophilic reaction mechanisms can be taken into consideration. Cycloaddition reactions involving unsaturated compounds—particularly those affecting ethylene and membrane unsaturated fatty acids—together with aromatic substitutions, reactions involving amine groups characteristic of amino acids, and ozonation processes leading to the formation of reactive oxygen species, may play an important role in carbohydrate alterations (Audran et al., 2018; Jamali et al., 2024).

3.1.1. Electrophilic ozone reaction with C═C bonds and role in ethylene and membrane unsaturated fatty acids oxidation

Ozone cycloaddition with unsaturated C═C bonds, known as the Criegee mechanism (Criegee, 1975), was clearly detailed in the work conducted by Cox et al. (2020) and illustrated in Fig. 2. The electrophilic cycloaddition of ozone to a C═C double bond leads to the formation of energy-rich molozonide (step 1), which undergoes rupture of the C—C bond and of one of the O—O bonds (step 2). Notably, for the sake of simplicity, only one of the two possible paths is shown in Fig. 2. As a result, the Criegee intermediate and a carbonyl compound are formed. These compounds can recombine giving rise to ozonide species which further decomposes into carbonyl compounds (not shown). On the other hand, the Criegee intermediate can also evolve according to different paths, which are highly dependent on the reaction conditions and on the nature and extent of the double bond substitution. In particular, formation of a vinyl hydroperoxide intermediate (step 3) has been reported along with the consequent generation of hydroxyl and vinoxy radicals (step 4). The latter reacts with molecular oxygen eventually forming stable carbonyl species and CO (Kroll et al., 2001; Vereecken et al., 2017). Another possible path is the rearrangement of the Criegee intermediate to dioxirane through ring closure (step 5). The latter evolves to several products including OH radicals, superoxide species, CO, CO_2, and alkyl molecules via a hot acid/ester intermediate. Finally, bimolecular reactions of the Criegee intermediate with H_2O, NO_2, CO or SO_2 have been also reported (step 6). Notably, reaction with water, which would be relevant to the aim of the present work, is comparatively slower than with the other mentioned molecules (Alam et al., 2013). In conclusion, a wide range of stable carbonyl or carboxyl compounds along with highly oxidizing radicals have been detected as a result of complex reaction of ozone with unsaturated compounds. For instance, the main products generated during reactions between ozone and most of the unsaturated hydrocarbons found indoor are formaldehyde, methacrolein and methyl vinyl ketone (starting from isoprene), 4-acetyl-1-methylcyclohexene (starting from limonene) and benzaldehyde (starting from styrene).

Through the above described cycloaddition, application of ozone can directly control the fruit softening process through the direct oxidation

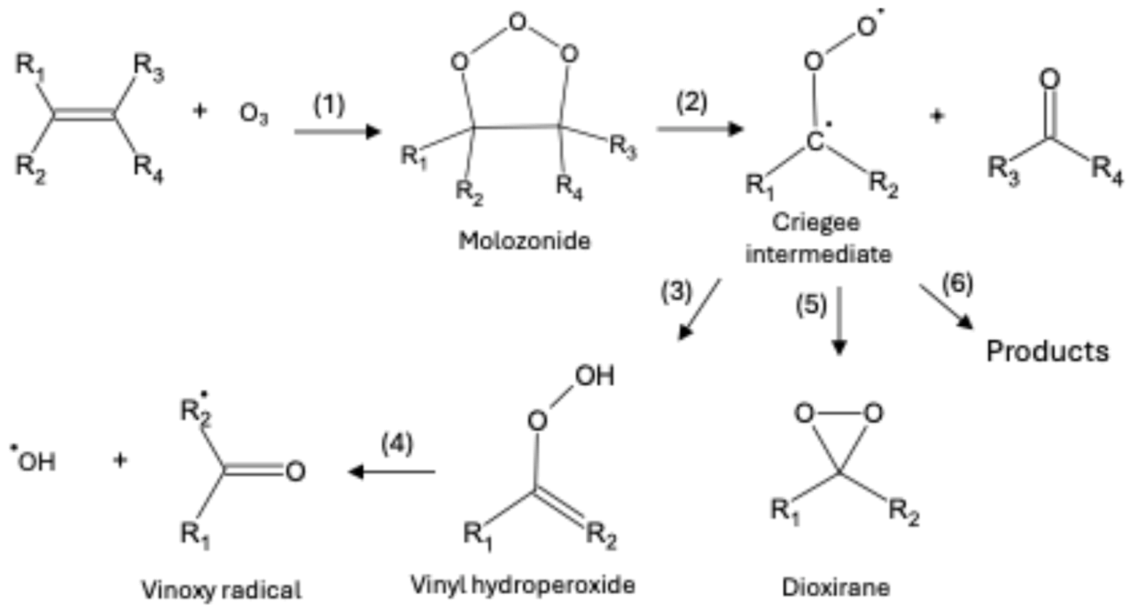

Fig. 2. Ozone cycloaddition mechanisms.
Step 1. Ozone undergoes electrophilic cycloaddition to the C═C double bond, leading to the formation of an energy-rich primary ozonide (molozonide).
Step 2. The molozonide rapidly decomposes through cleavage of the C–C bond and one of the O–O bonds, forming a carbonyl compound and a Criegee intermediate.
Step 3. The Criegee intermediate can evolve through different pathways depending on the reaction conditions and on the nature and extent of substitution of the double bond. One possible pathway involves the formation of a vinyl hydroperoxide intermediate.
Step 4. The vinyl hydroperoxide intermediate further decomposes, leading to the formation of hydroxyl (OH) radicals and vinoxy radicals. The latter reacts with molecular oxygen, eventually forming stable carbonyl compounds and CO.
Step 5. Alternatively, the Criegee intermediate can rearrange via ring closure to form a dioxirane intermediate. This species further evolves into several products, including OH radicals, superoxide species, CO, CO_2, and alkyl compounds, through a hot acid/ester intermediate.
Step 6. In addition, the Criegee intermediate can undergo bimolecular reactions with species such as H_2O, NO_2, CO, or SO_2.

of ethylene (C_2H_4).

The ozonolysis proceeds through the primary ozonide 1,2,3-trioxolane and mainly produces formaldehyde (HCHO), along with various other products such as ethylene oxide (EO), dioxirane, formic acid and hydroperoxymethylene (Alam et al., 2011; Wang et al., 2021):

$$C_2H_4 + O_3 \rightarrow CH_2OO^* + HCHO \quad (10)$$

where CH_2OO^* is the Criegee intermediate.

On the basis of the work conducted by Palau et al. (2001), the ethylene level in an empty 59.78 m^3 container, can be removed at a rate of 0.145 ppm h^{-1} over a 24 h period at 0 ± 1 °C and 1.3–2.1 ppm of O_3 (initial concentration of 3.8 ppm of ethylene) while a 0.4 μL L^{-1} O_3 concentration was effective in removing ethylene (lower than 1.0 μL L^{-1} during the first 20 days) from an apple and pear refrigerated storage room (Skog & Chu, 2001). Although ozone is considered a promising postharvest technology, some potential side effects should also be considered. In particular, ozone-induced ethylene oxidation may lead to the formation of formaldehyde, a toxic compound with antiseptic properties that could negatively affect fruit quality (Antora et al., 2018). Wang et al. (2021) reported that formaldehyde can be generated during ethylene oxidation under ozone treatment, although its accumulation may be partially limited by adsorption phenomena in fruits such as apples and bananas. In addition, low endogenous levels of formaldehyde are naturally present in several fruits and vegetables (Nowshad et al., 2018). Overall, these findings highlight the importance of carefully optimizing ozone concentration and storage conditions to maximize benefits while minimizing the formation of undesirable by-products.

Relevant ozone reactions with unsaturated C═C bonds take place directly at the surface of the horticultural products. Unsaturated fatty acids characterising phospholipids in the cell membrane can represent targets for O_3. The consequent alteration could produce positive effects when the technology is applied for microbial decontamination. Beyond its effects on fruit physiology and quality maintenance, ozone plays a primary role in the control of microbiological activity during postharvest storage. Due to its strong oxidizing capacity, ozone can inactivate a wide range of spoilage and pathogenic microorganisms, including bacteria and fungi. The antimicrobial mechanism involves oxidative damage to cell membranes, proteins, enzymes, and nucleic acids, causing cellular leakage and microbial death. Both gaseous and aqueous ozone treatments have shown efficacy in reducing populations of *Escherichia coli*, Salmonella spp., and Listeria monocytogenes, as well as fungal genera such as Aspergillus, Penicillium, and Fusarium. These effects, together with the absence of toxic residues after decomposition into oxygen, make ozone a promising strategy for enhancing postharvest microbial safety and shelf-life extension (Dubey et al., 2022; Xue et al., 2023).

Knowledge about the related oxidative degradation mainly comes from studies conducted at molecular level. For examples, reaction of low levels of ozone (20 ± 10 ppb) with 1-palmitoyl-2-oleoyl-sn-glycero-3-phosphocholine (POPC, 16:0 – 18:1 PC), resulted in formation of nonanal, nonanoic acid, and two ozone-induced oxidized lipids from POPC, in which the C═C bond is cleaved and replaced by an aldehyde (POnPC) or carboxylic acid (PAzPC). Authors evidenced that some products were released into the gas phase, while others could be readsorbed (Qiao et al., 2015).

3.1.2. Ozone aromatic substitution and amine group addition and role in amino acids oxidation

Electrophilic aromatic substitution eventually leads to aromatic ring opening and to the formation of different aliphatic products. The electron-donating properties of substituents on the aromatic ring, as OH, increase the reaction rate towards the ortho and para positions of the rings. In general, the initial attack of the ozone takes place mainly at those positions leading to the generation of dihydroxylated by-products, which are highly susceptible to further ozonation and final formation of quinoid compounds and aliphatic products containing carbonyl and carboxyl functions (Audran et al., 2018).

This mechanistic path is reported for amino acids like tyrosine tryptophan and histidine (Cataldo, 2006).

The amine functional group of amino acids undergoes addition at the lone electron pair of the nitrogen leading to the formation of R–N^{+}–O–O–O^{-} adducts. The homolytic rupture of these intermediates gives rise to the corresponding alkylhydroxylamines, which are then rapidly further oxidized to nitro-products (Essaïed et al., 2022).

3.1.3. Mechanisms of nucleophilic ozone attack and role in saturated organic substrates

Ozonation of saturated organic substrates containing C—H bonds, such as carbohydrates and fatty acids, leads to the formation of organic hydrotrioxide and dihydrogen trioxide (Yu et al., 2007).

The reaction can process via two major pathways. Ozone attacks on the C—H bond are 1,3-dipolar insertion and radical reactions, which involve ozone interacting with carbon and hydrogen atoms of differing partial charges. The 1,3-dipolar insertion mechanism occurs through the interaction between the partially positive carbon and partially negative oxygen atoms of ozone, leading to C–H bond cleavage. This process forms a transient hydrotrioxide (R–O–O–OH) intermediate, which then decomposes into alcohols, carbonyl and carboxyl compounds (eq. 13):

$$RH + O_3 \rightarrow (R - O - O - O - H)^* \rightarrow R\cdot + OH\cdot + O_2 \overset{O_2}{\rightarrow} ROH + R = O + ROOH \tag{11}$$

Notably, OH radicals are formed and can indirectly induce further oxidation. In particular, direct ozone attack on carbohydrates results in the production of carbonyl and carboxyl groups. Starting from studies conducted on model compounds (methyl-a-D-glucopyranoside, methyl-b-D-gluco-pyranoside, methyl-a-D-mannopyranoside, methyl-b-D-mannopyranoside and methyl-a-D-xylopyran), literature shows that the attack of β-glucoside involves the 1,3-dipolar addition to the anomeric carbon in the C–H bond, leading to the generation of hydrotrioxide (Olkkonen et al., 2000). These mechanisms can alter main constituents of the primary cell wall architecture through the alteration of polysaccharides as cellulose, hemicellulose, and pectin (Brummell, 2006).

3.2. Indirect oxidative mechanisms

Ozone is reported to indirectly oxidize organic compounds due to the action of reactive oxygen species (ROS) formed upon its decomposition or interaction with water. Following ozone degradation, several ROS as hydroxyl radicals (·OH), hydrogen peroxide (H_2O_2), superoxide radicals ($O_2\cdot^-$), and singlet oxygen ($^1O_2$) can be generated (Bi et al., 2024). These species are extremely reactive towards lipids, enzymes and proteins, and consequently could interact with microorganisms, ethylene and wall-modifying enzymes expressed during ripening (Wei et al., 2025).

However, contrarily to what often reported in literature, ·OH radicals formation through ozone reaction with water is efficient only at alkaline pH, thus making this path highly unlike both in humid gaseous phase of the postharvest environment and in the fruit product (Chu & Ching, 2003). Instead, as previously shown, ·OH radicals can be formed upon reaction of ozone with unsaturated and saturated compounds. Therefore, indirect oxidation mechanisms cannot be excluded when ozone interact with cell walls and plasma of horticultural products accessed through cuticle openings as lenticels or tissue cracks (Fares et al., 2010).

4. Effect of ozone in the control of the postharvest ripening, energy metabolism and elicitor effect

4.1. Regulation of fruit ripening

Fruit ripening is an amphibolic process that includes several anabolic and catabolic processes making the fruit suitable to disperse the seeds and human consumption. These biochemical and physiological modifications lead to significant alterations in several metabolic pathways, leading to the reprogramming of different primary and secondary metabolisms, finally determining change in color, aroma and taste. In parallel, important dismantling processes occur also in the cell wall, responsible for the mechanism of fruit softening that renders the fruit suitable for consumption but also more susceptible to pathogens attack (Bianchetti et al., 2024). According to differences evidenced in climacteric and non-climacteric fruit, the ripening process is ruled by endogenous (hormonal and transcriptional) and environmental factors (Cara & Giovannoni, 2008; Gapper et al., 2013). Especially in climacteric fruits, the production of ethylene plays a major role as starting signal in the coordination of the ripening process. In non-climacteric fruits, this role is more assigned to other hormones, mainly abscisic acid (Barry & Giovannoni, 2007; Perotti et al., 2023; Zenoni et al., 2023). Both endogenous and environmental factors interact to trigger and regulate the oxidative processes leading to modify important quality attributes, even with differences among species. As known, the softening and the weakening of the primary cell wall can be considered the main phenomenon affecting the postharvest and the main factor in determining possible deterioration of horticultural products (Giovannoni et al., 2017).

During ripening and storage, the principal event is the dismantling of the primary cell wall architecture composed of three main biopolymers, cellulose microfibrils held together by a diverse array of hemicellulose, in particular xyloglucan and glucomannan. This network is furthermore embedded in pectins, a complex heteropolysaccharide composed by homogalacturonan, xylogalacturonan, and two types of rhamnogalacturonan, and some structural glycoproteins and phenolics. Both covalent and non-covalent interactions between these components are the major event impacting on this structural network. The process of the cell wall disassembly involves the depolymerisation of glycans and the solubilization and depolymerization of pectins and loss of neutral side chains. As a consequence of the above cited reactions, cell walls are irreversible modified especially in terms of their mechanical properties, and, due to middle lamella dissolution, cell adhesion is significantly reduced (Brummell, 2006). These processes coordinately impact the fruit softening kinetics, playing an internal beneficial role for making the fruit suitable for consumption but also prone to senescence. These processes are catalysed by a discrete number of wall-modifying enzymes expressed during ripening. These include pectin degrading enzymes as polygalacturonase (PG), pectin methylesterase (PME, β-galactosidase (β-GAL), and pectate lyase (PL) and hemicellulose/cellulose-modifying enzymes such as 1,4-β-glucanase, xyloglucan transglycosy-lase/hydrolase (XTH) and expansin (EXP) (Paniagua et al., 2017), which are coordinated by transcription factors and epigenetic cues (Giovannoni, 2007; Yang et al., 2025).

4.2. Role of ozone in controlling ethylene biosynthesis and cell wall dismantling

The main goal of postharvest is to interfere with this process, extending storability and preventing fruit decay while promoting fruit quality. Application of ozone can directly or indirectly control the fruit softening process, by interfering with ethylene production or suppressing the expression of genes involved in both ethylene or cell wall metabolisms. As shown in Table 1, beside the direct oxidation of ethylene by ozone, exogenous application can inhibit the expression of ACS and ACO with a consequent reduction of ethylene (Shezi et al., 2020). According to previous results, treatment with ozone gas appears to decrease the biosynthesis of endogenous ethylene in kiwifruit, jackfruit and tomato by inhibiting *ACS1* and *ACO1* expression (Kartika et al., 2025; Minas et al., 2014,; 2018; Tzortzakis et al., 2013). However, relevant differences in type of food product (e.g., weight, surface area, and characteristics) and treatment conditions (e.g., ozone concentration, exposure time, and storage duration) across studies may influence

Table 1
Effect of ozone gas in terms of indirect and direct inhibition of cell wall degrading enzymes.

Type of inhibition	Product	Treatment condition	Result	Effect on other quality attributes	Reference
Indirect inhibition of the cell wall degrading enzymes	Kiwifruit	Ozone (0.3 μL L^{-1}) for 2 or 4 months (0 °C, 95% RH). Subsequent ripening (20 °C, 90% RH) for up to 8 days.	Inhibition of AdACS1 and AdACO1 expression and reduced ACC synthase (ACS) and ACC oxidase (ACO) enzyme activity.	_	(Minas et al., 2014)
	Kiwifuit	Ozone (0.3 μL L^{-1}) for up to 6 months (0 °C, 95% RH). Subsequent ripening (20 °C, 90% RH) for up to 14 days.	Reduced ACC oxidase (ACO) enzyme activity.	No effect in titratable acidity (TA) and dry matter content (DMC). Soluble solids concentration (SSC) increase was delayed.	(Minas et al., 2018)
	Jackfruit	Ozone (325–350 ppm) for 60 min at 13 °C for 20 days.	Inhibition of 1-aminocyclopropane-1-carboxylic acid (ACC) content and ACC synthase (ACS) and ACC oxidase (ACO) activities.	Maintaining fruit firmness, TSS, ascorbic acid content, and antioxidant activity (DPPH inhibition).	(Kartika et al., 2025)
	Tomatoes	Charcoal-filtered 'clean air' for 1 week prior to transferring to ozone (0.05 μmol mol^{-1}) for 1 more week.	Reduction of enzyme related to ethylene biosynthesis (1-aminocyclopropane-1-carboxylate oxidase-ACO).	_	(Tzortzakis et al., 2013)
Direct inhibition of the cell wall degrading enzymes	Kiwifruit	Ozone (0.3 μL L^{-1}) for 2 or 4 months (0 °C, 95% RH). Subsequent ripening (20 °C, 90% RH) for up to 8 days.	Inhibition of cell wall degrading enzymes activity, such as polygalacturonase (PG) and endo-1,4-*β*-glucanase/1,4- *β*-glucosidase (EGase/glu).	_	(Minas et al., 2014)
	Kiwifruit	Ozone (0.3 μL L^{-1}) for up to 6 months (0 °C, 95% RH). Subsequent ripening (20 °C, 90% RH) for up to 14 days.	Inhibition of the expression of ripening related genes, ethylene receptor (ETR1) lipoxygenase (LOX1), geranylgeranyl diphosphate synthase (GGP1), and expansin (EXP2).	No effect in titratable acidity (TA) and dry matter content (DMC). Soluble solids content (SSC) increase was delayed.	(Minas et al., 2018)
	Kiwifruit	Ozone (45 mg/m^3) every 12 h for 7 days (0 ± 1 °C).	Regulation of active genes xyloglucan endo glycosyltrans- ferase/hydrolase, cellulose synthase, polygalacturonase, and PE.	Increments in firmness and delaying in the decrease of titratable acid content and the increase of SSC content.	(Wang et al., 2024)
	Cantaloupe	Ozone (0.15 ppm during the day and 0.3 ppm overnight) for a maximum of 13 day (6 °C, 90% RH).	Reduced activities of cell wall enzymes *α*-arabinopyranosidase, *β*-galactopyranosidase and polygalacturonase.	No effect in colour, titratable acidity (TA), totals soluble solids (TSS), carotenoid and ascorbic acid contents. Increment in firmness.	(Toti et al., 2018)
	Cantaloupe	Ozone (21.4–149.8 mg/m^3) 12 h on, 12 h off for 15 days (15 °C).	Inhibition of the activity and gene expression of polygalacturonase (PG), pectin methylesterase (PME), *β*-galactosidase (*β*-gal), cellulose (Cx), and *α*-L-arabino- furanosidase (*α*-L-Af).	Reduction of the respiration rate intensity. Increments in firmness and in total soluble solids (TSS).	(Peng et al., 2024)
	Tomato	Ozone (10 μL/L) for up to 20 min. Subsequent ripening (20 °C, 90% RH) for up to 9 days.	Decreased pectin and polyuronide depolymerization. A decrease in pectin methyl esterase (PME).	No effect in colour, sugar content, acidity and antioxidant capacity. Reduction in damages, weight loss and accumulation of phenolic compounds.	(Rodoni et al., 2010)

the extent of inhibition.

Concerning enzymes and related genes directly driving the cell wall structure alterations during ripening, ozone gas treatments play a significant role in the inhibition of cell wall degrading enzymes activity. As detailed in Table 1, the inhibition of polygalacturonase (PG) and endo-1,4-β-glucanase/1,4-β- glucosidase were observed (EGase/glu) (Minas et al., 2014). In addition, the expression of several kiwifruit ripening genes as ethylene receptor (ETR1), lipoxygenase (LOX1), geranylgeranyl diphosphate synthase (GGP1), and expansin (EXP2) seems highly affected by ozone treatments (Minas et al., 2018). In cantaloupe, the activity and gene expression of PG, pectin methylesterase (PME), β-galactosidase (β-gal), cellulase (Cx), and α-L-arabino- furanosidase (α-L-Af), were inhibited under ozone treatments with a consequent suppression of the degradation of cell wall components associated with fruit softening (protopectin, soluble pectin, cellulose, and hemicellulose) (Peng et al., 2024; Toti et al., 2018). The exposure to ozone gas involves, in tomatoes, a decrement in pectin solubilization, and a higher accumulation in uronic acids than neutral carbohydrates. In addition to this, any changes in hemicellulose polysaccharides and a decrease in PME, which have a role in the modulation of pectin depolymerization, were observed (Rodoni et al., 2010). These results, even if focused on a limited type of products and operative parameters conditions provide a foundation for understanding the effect of ozone treatment in terms of molecular alteration and key genes involved in delaying senescence.

4.3. *Ozone interaction with the mitochondrial activity*

The multiple roles of mitochondrial energy status in regulating postharvest physiological activities, playing a significant role in delaying senescence while preserving quality of fruit and vegetable during storage, has been already proposed (Prusky et al., 2025). When ozone gas interacts with horticultural products it appears to have a positive effect on mitochondrial metabolism which result in a reduced loss of energy charge and adenosine-5′-triphosphate (ATP) in the product during storage, with increments in the activity of enzymes involved in oxidative phosphorylation (Piechowiak et al., 2021b). The increased activity of mitochondria seems to promote mitochondrial ROS accumulation as superoxide anion radical ($O_2\cdot^-$), hydroxyl radical (·OH, H_2O_2, and singlet oxygen $^1O_2$). The accumulation of these radicals in the mitochondria is normally associated to a decrease in the respiration intensity (Piechowiak et al., 2021a).

Ozone, depending on its concentration, can presents, however, a double role in the mitochondrial activity, influencing the quote of energy production. This can also be regulated by ethylene, for its ability to control the aerobic respiration occurring in the mitochondria. The production of adenosine-5′-triphosphate (ATP) through oxidative phosphorylation is the recognised fundamental factor for the resistance and inhibition of stresses of horticultural products during postharvest storage (Piechowiak et al., 2021a, 2021b). The main enzymes involved in mitochondrial energy metabolism include succinate dehydrogenase (SDH), cytochrome C oxidase (CCO) and H+–ATPase. SDH, an enzyme of the respiratory chain complex II, catalyses succinate dehydrogenation leading to the formation of fumarate, while CCO is active in collecting electrons from cytochrome c, transferring them to an oxygen molecule and leading to the formation of H_2O molecules through the attachment of H^+ ions in complex IV of electron transport chain (ETC). Finally, H+–ATPase facilitates ATP breakdown into ADP with a release of energy necessary to create a transmembrane electrochemical gradient for proton transport during ATP biosynthesis (Shezi et al., 2020; Zhou et al., 2014). In literature, several works evidenced an overall higher level of ATP in ozonated fruit, and a higher activity of enzymes involved in oxidative phosphorylation SDH, CCO and H^+– ATPase.

By treating blueberry fruit with ozone gas (15 mg L^{-1} for 30 min every 12 h), an increase in ATP level of about 23% was observed after 7 days of storage at 4 °C respect to control associated with an increase of SDH (58.7%), CCO (118.2%) and H+-ATPase (78.16%). The level of ATP of both samples gradually decreased in the subsequent 21 days of storage, even if the amount of adenosine diphosphate (ADP) and energy charge (EC) of ozonated samples was higher compared to control ones (Piechowiak et al., 2021b). Similarly, ozone treated in raspberries (8–10 mg L^{-1} for 30 min every 12 h), inhibited the loss of energy status at room temperature (20–25 °C). In ozonated samples any significant changes in the contents of ATP and ADP and energy charge (EC) were observed after 24 h of storage, in contrary, control fruit showed a decreased pattern (56.6, 59.5, and 76.7%, respectively). In general, in terms of activity of enzymes, the ozonation is responsible of significant increase after 24 h (42% for SDH) to gradually decline thereafter until 72 h of storage (Piechowiak et al., 2021a).

The effects of ozonation treatment on energy level were also indirectly explored by assessing the poly-(ADP-ribose) polymerase 1 gene expression (PARP-1) and at the related NADPH metabolism in strawberry fruit (Piechowiak et al., 2022). PARP activity, by detecting and beginning cell response to single-strand DNA damage using NAD^+ as substrate, is associated to the resistance of plant to both biotic and abiotic stress. By increasing PARP activity, a loss in NAD^+ contributes to a reduction in NADPH and ATP (Aghdam & Alikhani-Koupaei, 2021). Following ozone gas treatments in strawberry (10–100 ppm for 30 min at 20–22 °C every 12 h), an initial increase (after 1 day of storage) in the levels of NAD^+ (17.4%) and NADH (24.2%) was reported only for 10 ppm concentration. In subsequent storage periods, a gradual decline in the level of NAD^+ and NADH was shown. The observed decrement in NADH is connected to a decrement in the content of reduced glutathione and consequently to a higher level of ROS in the tissue. In addition, after 1 day of storage, the expression of PARP-1 in the ozonated fruit was higher (up to 2.8 times) than the control fruit by 2.8 and 1.7 times and continues to increase during the explored 3 days of storage (Piechowiak et al., 2022).

Ozone, by increasing the energy metabolism, can also stimulate a higher generation of ROS together with the expression of genes deputed to encode enzymes with antioxidant activity. These enzymes are represented by superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), glutathioneperoxidase (GPX) and peroxidase (POD). In addition to the enzymatic scavenging pathway, there are numerous antioxidants, such as carotenoids, ascorbic acid (AsA), and glutathione (GSH) playing a significant role in the homeostatis regulation. In the study carried out on blueberries, the ozone treatment increased the production of ROS by 58%, after 7 days of storage. The activity of SOD and GPX, after 7 days of storage were higher in ozonated samples than control (Piechowiak et al., 2021b). A similar behaviour was also observed in raspberry, where the application of ozone during 48 h of storage increased the levels of superoxide anion radical ($O_2\cdot^-$) and hydrogen peroxide (H_2O_2) together with the activity of SOD in mitochondria (Piechowiak et al., 2021a). Treatment with ozone induced CAT, SOD and POD enzymatic activity in cold stored kiwifruit that, compared to control, exhibited a lower production of $O_2\cdot^-$ and H_2O_2 and therefore a higher inhibition of postharvest oxidation phenomenon and a better storability. These results shed light on the mechanisms through which ozone influence the mitochondrial functionality by regulating oxidative stress and antioxidant defence. This can also occurs by the modulation of the expression of genes associated with antioxidant enzymes and ascorbate-glutathione ASA-GSH metabolism was shown (Wang et al., 2023).

4.4. The application of ozone can regulate the production of bioactive compounds with antioxidant activity

Recent reviews on ozonation as a method of abiotic elicitation summarise the effect of the treatment on health promoting properties of plants with particular attention to increments in production of polyphenols and ascorbic acid (Bianchetti et al., 2024; Kaur et al., 2022; Sachadyn-Król & Agriopoulou, 2020). However, a critical analysis of the cited literature points out some important concerns about the dosage of ozone, duration of treatment, type of fruits and vegetables, and time from harvest to interaction with ozone. Particularly, several results evidenced a positive role in the increment of bioactive components following ozone applications at a relatively low concentration for a short time immediately after harvest. On the basis of the work conducted on Andean Blackberries by Horvitz et al. (2024), low concentrations of gaseous O_3 (0.4–0.7 μLL^{-1} for 3 min), used in a single application before storage, promoted the synthesis of biocompounds and was effective in maintaining the postharvest quality of fruit for at least 4 days of refrigerated storage. The highest concentration (0.7 μLL^{-1}) produced instead an excessive oxidative stress, enhancing antioxidant activity and bioactive compounds content only until day 1 of storage. An opposite scenario was also observed in papaya fruit in terms of activity of plant defence enzymes, such as phenylalanine ammonia-lyase (PAL), peroxidase (POD) and polyphenol oxidase (PPO), depending by the level of ozone, suggesting a concentration of 3.5 μLL^{-1} for 96 h prior to ambient storage (Ong et al., 2014). High ozone doses or long treatments can produce an over-oxidation and consequently a reduction in the phenolic content, probably due to direct reactions with ozone and related or with hydroxyl radicals produced through ozone decomposition (Kaur et al., 2022). For instance, grapevine short-term treated with ozone (1.5 g/h for 18 h) preserved their phenolic and anthocyanin contents, while, long-term treatments (1.5 g/h for 4 h each day during dehydration) caused a decrease in both compounds (Botondi et al., 2015). Similarly, also fruit of raspberry treated with high concentration of ozone (0.9 respect to 0.3 mg/L) for 120 min (instead of 60 min) was characterized by a decreased phenolic concentration (Onopiuk et al., 2017). This phenomenon can have a detrimental effect because an excessive production of ROS, exceeding the scavenging capacity of the antioxidant system, can generate an oxidative damage in the fruit.

5. Potential strategies for the improvement of the shelf life of the horticultural products and future directions

By providing a comprehensive examination of the ozone-horticultural products interaction during postharvest storage and by going in depth into main realistic oxidative mechanisms, the present review highlighted the potential application of ozone as a valid strategy in postharvest storage applications to promote quality and storability of fresh produce.

The analysis of the mechanisms driving ozone gas generation and the consequent decomposition in the closed air space, evidence that different variables should be however specifically controlled. The generation of ozone for postharvest application must be optimized taking into account different factors, such as oxygen flow rate, temperature, relative humidity, storage room loading, chemical and physical properties of the stored produce and the gas composition into the storage room. Due to the cell molecular characteristics, different types of horticultural products and relates physiological and microbiological states can involve different interaction with ozone. Further knowledge on O_3 decomposition reaction kinetics in the presence of horticultural products is mandatory for the setting up of operative parameters in terms of levels of ozone concentration, treatment durations, storage conditions, and method of application (continuous or intermittent).

Moreover, great part of literature is related to experiments conducted on small or lab scale storage, while the possible technical aspects related to the distribution of the gas in commercial postharvest storage rooms are still very scarce, limited and associated to the lack in the knowledge in the decomposition kinetics. For a reliable transfer of the technology, further studies conducted in a semi-scale system underlining which active sites of the product surface accelerate the gas degradation and how the gas move through the mass, can clarify how distribute ozone in commercial storage rooms. The ozone distribution is consequently affected, apart from room storage conditions and characteristics, by the above cited active sites.

Additional knowledge is also needed to investigate the role of ozone in combination to other postharvest strategies currently applied to improve storage of horticultural produce, such as low oxygen-controlled atmosphere (CA or DCA) or 1-MCP. Based on the state of the art, it is not clear how to alternate O_3 treatments with already established postharvest strategies.

However, a pre-treatment with ozone could have positive effects on the microbial decontamination and in the biosynthesis of low-molecular-weight antioxidants and, consequently, on the other storage processes.

The adoption of ozone as postharvest strategy shows several important challenges related to both maintenance of the storage room and related equipment, and safety of workers. Its instability requires the adoptions of dedicated materials resistant to the possible induced oxidation by avoiding those characterised by rubbers, neoprene, latex paint and linoleum, with increments in the cost of the facilities management. In terms of safety of workers, a system for ozone removing before the storage room opening is mandatory. For residuals, the occupational exposure limit value (OELVs) may vary between country and typically range from 0.05 to 0.1 ppm for a long term (8 h time on average) and 0.3 ppm for short-term exposure (15 min) (EFSA, 2021; Grignani et al., 2020).

Glossary

Controlled atmospheres (CA)	Storage of fruit in an atmosphere with controlled concentrations of oxygen and carbon dioxide, as well as the temperature and humidity
1-Methylcyclopropene (1-MCP)	An inhibitor of ethylene action that interacts with receptors in plant cells
Aminoethoxyvinylglycine (AVG)	A synthetic compound acts as an inhibitor of ethylene biosynthesis
Dielectric barrier discharge (DBD)	A non-thermal plasma generated by applying high voltage between two electrodes, one of which is covered by a dielectric
Microdischarges	Short-lived, high-intensity plasma filaments formed in small gaps in DBD
Non-thermal plasma (NTP)	A non-equilibrium plasma with hot electrons and relatively cold ions and neutrals
Criegee mechanism	The fundamental pathway of ozonolysis is where ozone (O_3) breaks unsaturated hydrocarbons
Criegee intermediate	Highly reactive intermediates are formed during ozonolysis of alkenes
Reactive oxygen species (ROS)	Highly reactive oxygen-derived molecules, such as $\cdot OH$, H_2O_2, $O\cdot_2^-$, $^1O_2$
Occupational exposure limit value (OELVs)	The maximum limitation concentration of a hazardous substance which worker can be exposed to without negative side effects

Ethical statement

The authors declare that no studies in humans and animals were conducted in this paper.

CRediT authorship contribution statement

Nadda Khongsay: Writing – review & editing, Writing – original draft, Conceptualization. **Alessandro Gottuso:** Writing – review & editing. **Francesco Parrino:** Writing – review & editing, Supervision. **Angelo Zanella:** Writing – review & editing. **Fabrizio Costa:** Writing – review & editing, Supervision. **Annachiara Berardinelli:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Annachiara Berardinelli reports article publishing charges was provided by University of Trento. Annachiara Berardinelli reports a relationship with University of Trento that includes: employment. Annachiara Berardinelli has patent no patent pending to no patent. no additional relationships or activities to declare If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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