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OZONE STRESS IN PLANTS: SIGNALLING AND RESPONSE

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Abstract

Ozone (O_3) pollution is a serious global environmental threat, with tropospheric ozone levels frequently classified as some of the most toxic air pollutants. Elevated tropospheric ozone levels affect vital processes in plants, encompassing respiration, photosynthesis, and nutrient uptake, thereby causing a decline in plant growth and development. Plants display a complex set of defense strategies against O_3 stress, including stomatal regulation of O_3 influx into leaves, photosynthetic adjustments, modulation of antioxidant defense against O_3-induced reactive oxygen species (ROS), and secondary metabolism. Stomatal closure is the first response to O_3 stress in most plants, providing protection from high O_3 influx to the leaves. One negative outcome of this is the decreased influx of CO_2 into the leaves, resulting in a decline in the photosynthetic rate. In response to O_3 stress, plants strive to adjust their photosynthesis by regulating the photosynthetic electron transport chain through photorespiration, cyclic electron flow, or the alternative oxidase pathway, while also enhancing anthocyanin production to protect their photosynthetic systems. Plants are also equipped with a substantial antioxidant defense system that consists of both enzymatic and non-enzymatic antioxidants, which work together to neutralize the excess O_3-induced ROS. This review summarizes recent advances in understanding the strategies that plants use to protect their structural and functional integrity in response to O_3 pollution.

Key words: *air pollution, antioxidant defenses, photosynthetic adjustments, stomatal regulation.*

INTRODUCTION

In the last several decades, global patterns of industrialization and rapid urbanization have led to an increase in the production of air pollutants, adversely affecting living organisms (Antenozio et al., 2024). Air pollutants refer to all substances in the air, whether inorganic or organic, that compromise air quality, generating adverse impacts on the environment (Stoykova et al., 2025). They can be classified into two categories: primary and secondary, depending on their source (Manisalidis et al., 2020). Primary pollutants, including carbon oxides, sulfur oxides, nitrogen oxides, particulate matter, and volatile organic compounds, are released directly from identifiable sources, whereas secondary pollutants are not released directly; instead, they are generated in the atmosphere through chemical reactions that involve primary pollutants and other air components such as water vapor or oxygen. A notable example is tropospheric ozone (Bălă et al., 2021; Cadar et al., 2023). Ozone (O_3) is an allotrope of oxygen, consisting of three oxygen atoms. The atmosphere contains two areas where O_3 exists: the stratosphere and the troposphere, both of which share the same chemical composition (Alvim-Ferraz et al., 2024). Most of the O_3, approximately 90%, is formed naturally in the stratosphere as a result of ultraviolet radiation interacting with O_2. Specifically, the interaction of ultraviolet rays with O_2 in the stratosphere leads to the splitting of the O_2 into two single oxygen atoms. A released oxygen atom then binds with O_2 to create an O_3 molecule (Bernhard et al., 2023).

Stratospheric O_3 is extremely important for life on Earth, as it prevents a large part of harmful ultraviolet radiation from reaching the Earth's surface. Regrettably, over the past few decades, human activities have notably led to the destabilization of the stratospheric ozone layer. The consequences of stratospheric O_3 depletion are manifested through the appearance of ozone holes, which are considered to be, among other things, a result of the adverse effects of various human-made chemicals such as chlorofluorocarbons, methyl bromide, carbon tetrachloride, and methyl chloroform (Chipperfield & Bekki, 2024).

O_3 in the lower atmosphere (tropospheric ozone), is created through intricate chemical reactions involving nitrogen oxide gases and volatile organic compounds under sunlight. In this context, it is necessary to note that the production of tropospheric O_3 is positively associated with sunshine hours and negatively associated with both relative humidity and wind speed. As a result, the concentration of O_3 varies throughout the season and even within the day, exhibiting higher levels during the daytime and in dry months, particularly in areas close to industrial facilities (Nowroz et al., 2024).

Tropospheric O_3 is extremely harmful to both humans and animals. Its inhalation, even at relatively low levels, can result in respiratory tract inflammation, migraines, burning eyes, irritation of mucous membranes, chest pain, and asthma attacks (Kim et al., 2020). O_3 is also highly toxic to plants. The effect of O_3 on plants is reliant on its concentration as well as the duration of exposure. Long-term exposure to low levels of O_3 impairs stomatal function, disrupts nutrient uptake and respiration, and decreases the photosynthetic rate, often without any evident destruction to the plant tissues. Conversely, short-term exposure to high levels of O_3 results in the initiation of visible lesion formation in leaves (Wang et al., 2024). These disturbances negatively influence plant development and reproductive success, ultimately resulting in lower crop yields and compromised quality. Over the past century, tropospheric O_3 levels have risen by 2 to 3 times, which implies that more severe and widespread challenges due to O_3 are likely to increase in the future (Donzelli & Suarez-Varela, 2024).

Several studies have demonstrated that plants adapt to O_3 pollution by undergoing changes in their molecular, biochemical, and physiological responses, involving large-scale changes in enzyme activities and gene expression (Günthardt-Goerg et al., 2023; Rao et al., 2025). It is also well documented that reactive oxygen species (ROS) generated from the breakdown of O_3 in the extracellular space (apoplast) activate multiple signaling pathways that are seamlessly integrated within the cell into a delicately balanced ROS signaling network, which is crucial for the plant's response to O_3 stress (Vainonen & Kangasjärvi, 2015). Despite the extensive research in this area, many of these signaling pathways against O_3 stress are still not well comprehended. Addressing these knowledge gaps is important for a deeper understanding of how plants react to O_3 stress and for creating strategies to reduce and control O_3 pollution, particularly in urban areas. This review summarizes recent advances in understanding the strategies that plants use to protect their structural and functional integrity in response to O_3 pollution.

OZONE STRESS SIGNAL PERCEPTION AND TRANSDUCTION IN PLANTS

Several investigations into plant responses to O_3 pollution have confirmed that O_3, once it enters leaves through stomata, stimulates the excessive production of ROS in the apoplast, including superoxide anion radicals (O_2^-), singlet oxygen ($^1O_2$), and hydrogen peroxide (H_2O_2) (Podgórska et al., 2017; Montes et al., 2022; Yu & Blande, 2022; Simin et al., 2026). Furthermore, it is thoroughly documented that O_3 triggers plasma membrane-bound NADPH-dependent oxidases to create ROS (Sachdev et al., 2021). It is also noted that O_3 and H_2O_2 can diffuse directly into the cytosol through aquaporins, resulting in the generation of further ROS (Aranda-Rivera et al., 2022).

The overproduction of O_3-induced ROS may initiate a wide array of cellular changes, including depolarization of the plasma membrane, alterations in cell wall compounds, ozonolysis of double bonds present in the unsaturated fatty acids in cell membranes, and the activation of signal transduction proteins within the plasma membrane. Thus, the way in which plant cells perceive O_3 might be related to the to the modifications in cell walls and plasma membranes resulting from O_3-induced ROS (Rebouças et al., 2017). In this context, Kangasjärvi et al. (2005) indicated that three distinct mechanisms may play a role in O_3/ROS sensing. These include the generation of lipid-based signaling molecules that result from the oxidation of plasma membrane lipids, alterations in the cellular redox balance caused by the interaction of O_3/ROS with redox-active compounds, and the activation of apoplastic receptor proteins that are directly altered by

ROS. Once the sensing process is complete, the signals generated at the membrane-bound receptors or sensors are transformed into cellular responses through a series of signal transduction pathways, including Ca^{2+} signaling pathways and mitogen-activated protein kinase (MAPK) cascades, in addition to numerous plant hormone-dependent pathways (Hasan et al., 2021).

It is also well documented that the signal from apoplastic ROS can be transmitted to the chloroplast via membrane-associated heterotrimeric G proteins, resulting in the subsequent production of chloroplastic ROS. The generation of ROS in chloroplasts also leads to the activation of multiple downstream signaling pathways that may work in parallel, in series, or through a combination of both (Shapiguzov et al., 2012).

Baier et al. (2005) reported that the ozone stress signal transduction in plant cells consist of a two-step process: (1) rapid signaling events that involve Ca^{2+} influx and protein phosphorylation reaction from upstream receptor to downstream target, and (2) the activation of plant hormone-dependent pathways that serve to stabilize and enhance the plant's defense response to O_3 stress.

The influx of Ca^{2+} ions from the apoplast into the cytosol through plasma membrane represents the initial step in ozone stress signal transduction in plant cells, occurring in only a few minutes. This event results in an increase in cytosolic-free Ca^{2+} concentration, which then induces rapid changes in the protein phosphorylation pattern (Lee et al., 2021). Phosphorylation reactions are fundamentally significant in signal transduction pathways, facilitating signal transduction and integrating various signaling routes. Protein phosphorylation by specific mitogen-activated protein kinase (MAPK) cascades acts as a crucial pathway that functions downstream of sensors and receptors, translating extracellular signals into intracellular reactions in plant cells when exposed to O_3. Each MAPK cascade consists of three kinase modules: MAPK kinase kinases (MAPKKKs), MAPK kinases (MAPKKs), and MAPKs, which are interconnected in different manners to upstream receptors and downstream targets (Majeed et al., 2023). A pathway by which Ca^{2+} influx leads to the activation of the MAPK pathway is well documented. In short, increases in cytosolic free Ca^{2+} levels trigger MAPKKKs, which subsequently phosphorylate MAPKKs. The activated MAPKKs further phosphorylate MAPKs, which, in turn, can activate a diverse range of transcription factors (Lin et al., 2021).

Significant progress in associating MAPKs with O_3 stress signaling have emerged from the examination of the model plant *Arabidopsis thaliana* (L.) Heynh. Jagodzik et al. (2018) reported that the *A. thaliana* genome encodes 20 MAPKs, 10 MAPKKs, and 80 MAPKKKs genes. The high number of distinct kinases within the plant genome points to a likely complexity and interaction among MAPK cascades (Sun & Zhang, 2022). In the *A. thaliana* MAPK signaling pathways, two well-known MAPKs, MAPK3 and MAPK6, serve as crucial regulators that are activated in reaction to O_3 stress (Jiang et al., 2025). Their activation occurs within a period of 10 to 30 minutes after O_3 exposure, highlighting it as one of the earliest events in intracellular signaling. Once activated, MAPK3/6 translocate into the nucleus, where they regulate the expression of specific genes responsible for the synthesis of various stress-related proteins (Yadav & Mina, 2022). Several studies have shown that a considerable similarity exists in the gene expression patterns observed in plants exposed to O_3 and those showing responses to pathogen attack, suggesting that O_3-induced ROS may initiate programmed cell death (PCD) similar to a hypersensitive response in plant pathogenesis (Leppälä et al., 2022). PCD refers to an active and genetically regulated process through which plants eliminate unwanted and potentially harmful cells. It is also a common feature in plant development: it can be observed during floral organ abortion, senescence, tracheary element formation, and the formation of aerenchyma. The prevailing assumption is that O_3-initiated PCD acts as an initiator for lesion formation in leaves, which in turn limits the spread of oxidative bursts triggered by O_3 degradation in the apoplast (Bartoli et al., 2013). O_3-induced PCD is a highly organized process that is regulated by a complex network of signaling pathways, including those activated by plant hormones. Multiple research studies have demonstrated

that the accumulation of salicylic acid (SA) in O_3-exposed plants is correlated with the formation of leaf lesions, suggesting that SA plays an important role in O_3-induced PCD (Tamaoki, 2008; Poór, 2020; Modesti et al., 2023). Faoro and Iriti (2009) noted that SA can suppress H_2O_2-scavenging enzymes, thus promoting the adverse effects of ROS on plant cells, leading to PCD. Plant exposure to O_3 also activates signaling pathways that result in an increased accumulation of ethylene (ET) in plant cells (Guo et al., 2018). MAPK3/6 play a significant role in regulating ET production, as they are involved in the phosphorylation of aminocyclopropane-1-carboxylic acid synthase (ACCS), which is crucial for ET synthesis (Liu & Zhang, 2004). This leads to increased cellular ACCS activity and, as a result, enhanced ET production. It is generally accepted that ET has a role similar to that of SA in O_3-induced PCD; however, there are doubts about whether it carries out this function in conjunction with SA or independently (Vahala et al., 2003). The hypothesis that both SA and ET together modulate cell death in O_3-sensitive plant genotypes, and that O_3-induced ET synthesis is a result of increased cell death caused by SA, is widely accepted among scientists (Grantz & Vu, 2012; Xu et al., 2015). The heightened synthesis of jasmonic acid (JA) and its methyl ester, methyl jasmonate (MeJA), is another outcome of exposing the plant to O_3 stress (Rehman et al., 2023). Li et al. (2022) noted that JA derivatives are involved in limiting lesion spreading by antagonizing the cell death-promoting functions of SA and ET. This aligns with the conclusions presented in two previous studies (Rao et al., 2000; Zhou et al., 2020). Numerous studies have also confirmed that foliar abscisic acid (ABA) levels also escalate rapidly once plants are exposed to O_3 (McAdam et al., 2017; Guo et al., 2020; Xu et al., 2026). It is assumed that ABA plays a role in the response to O_3 stress by stimulating guard cells to close stomata, thereby reducing the likelihood of O_3 entry and lesion initiation (Kashtoh & Baek, 2021). However, recent studies have shown a decrease in stomatal sensitivity to ABA depending on ET, highlighting the antagonistic roles of ABA and ET in regulating stomatal movement when plants are faced with O_3 stress (Wilkinson & Davies, 2010; Müller, 2021). As an illustration, in various plant species, ET is noted to promote stomatal opening, consequently hindering ABA-induced stomatal closure (Song et al., 2023; An et al., 2025; Huang et al. 2025). Figure 1 displays a simplified schematic diagram that depicts the key signaling pathways related to plant responses under O_3 stress.

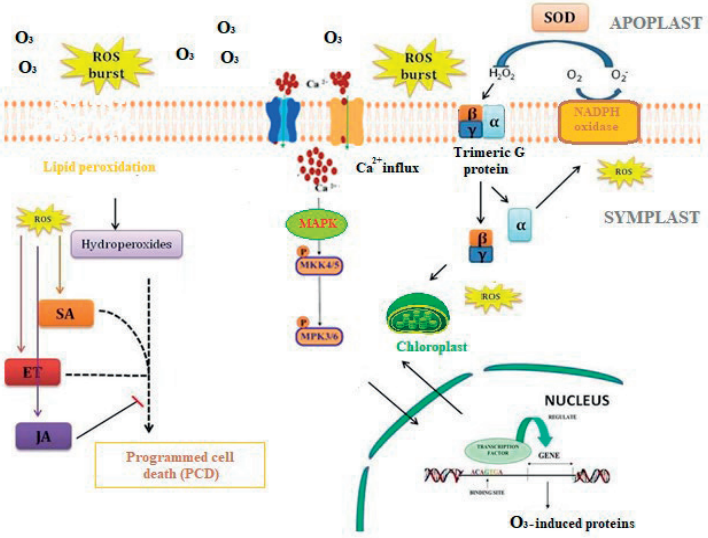


Figure 1. A schematic diagram of the key signaling pathways involved in the plant's response to O_3 stress

PLANT DEFENSE MECHANISMS AGAINST OZONE STRESS

Plants display a complex set of defense strategies against O_3 stress, including stomatal regulation of O_3 influx into leaves, photosynthetic adjustments, modulation of antioxidant defense against O_3-induced reactive oxygen species (ROS), and secondary metabolism.

Stomatal regulation

Stomatal closure is the first response to O_3 stress in most plants, which occurs within a few minutes of being exposed to O_3, thereby restricting the uptake of O_3 through the stomata. The anion channels in guard cells are crucial in controlling the size of stomatal pores (Chen et al., 2022). There are two categories of anion channels found in the plasma membrane of guard cells: R (rapid)-type and S (slow)-type, both activated in guard cells by the stress hormone ABA. Specifically, upon exposure to O_3 stress, guard cells show a substantial rise in ABA and ROS levels, which initiates a cascade of signaling events that activate anion channels. The outcome of this activation is the efflux of ions (K^+, Cl^- and malate) from the guard cell, which ultimately decreases turgor pressure, thereby resulting in the closure of the stomata (Saito & Uozumi, 2019).

The S-type slow anion channel 1 (SLAC1) is recognized as one of the significant and extensively studied anion channels (Deng et al., 2021). The plant hormone ABA initiates the activation of SLAC1 via a signaling pathway that includes ABA receptors and protein phosphatase 2C (PP2C). These components are involved in the activity of Ca^{2+}-independent kinase Open Stomata 1 (OST1) along with various Ca^{2+}-dependent protein kinases that phosphorylate SLAC1 (Bharath et al., 2021). SLAC1 phosphorylation may also take place via an ABA-independent signaling pathway, which is triggered by O_3-induced ROS and facilitated by Ca^{2+}-dependent protein kinases (CDPKs) (Munemasa et al., 2015).

Despite the fact that stomatal closure under O_3 stress conditions is very beneficial for the plant's survival by minimizing O_3 uptake and its damaging oxidative effects, it should not be ignored that this closure has a detrimental effect on photosynthesis as a result of reduced CO_2 intake (Lee et al., 2021). Additionally, O_3-induced ROS can cause harm to the chloroplast ultrastructure and interfere with the photosynthetic electron transport chain, thereby further hindering the photosynthetic rate. As a consequence, plant growth and development are adversely impacted (Ramya et al., 2021).

Photosynthetic adjustments

O_3-tolerant plants possess inherent defense mechanisms that enable them to adjust photosynthesis to O_3 stress, thus reducing the damage that arises from O_3. The main mechanisms encompass the regulation of the photosynthetic electron transport chain, the increase in anthocyanin production to protect the photosynthetic apparatus, and the regulation of photosynthetic protein transcription (Upadhyay et al., 2025).

The regulation of the photosynthetic electron transport chain under O_3 stress conditions can be achieved through photorespiration, cyclic electron flow, and the alternative oxidase pathway. These mechanisms work in unison to protect the plants from photoinhibition and maintain cellular redox homeostasis within the cell.

Photorespiration starts with the oxygenation of ribulose-1,5-bisphosphate (RuBP) resulting in the formation of 3-phosphoglycerate (3-PGA) and 2-phosphoglycolate (2-PG), which is partially recycled into the C_3 cycle through the photorespiration pathway. This process is commonly seen as a wasteful process because it generates 2PG, a compound that is harmful to numerous enzymes involved in photosynthetic metabolism, and it oxidizes organic carbon without apparently producing ATP (Shi & Bloom, 2021). However, under stressful conditions, photorespiration is of exceptional importance for plant functionality for several reasons. First, photorespiration acts as a protective mechanism to dissipate excess light energy, safeguarding the photosynthetic machinery from photoinhibition (Smith et al., 2024). Second, the oxygenation of RuBP requires large quantities of ATP and NADPH, resulting in the regeneration of ADP and $NADP^+$, which are crucial for the light-dependent reactions of photosynthesis (Nazari et al., 2024). Third, glycine, generated as the

ultimate product of photorespiration, is required for the synthesis of glutathione, a crucial part of antioxidant defense systems in plants (Voss et al., 2013).

Cyclic electron flow (CEF) serves as another protective mechanism for photosynthetic apparatus under O_3 stress. During CEF, electrons are recycled through photosystem I, leading to the production of ATP without concomitant production of NADPH, thus raising the ATP/NADPH ratio essential for the Calvin cycle (Wang et al., 2023a). Additionally, CEF helps to prevent the excessive reduction of the acceptor side of photosystem I (PSI), consequently reducing the generation of superoxide anion radicals and protecting PSI from photoinhibition (Cun et al., 2022).

Maintaining a fine balance between energy production and utilization is fundamentally significant for plants' survival in adverse conditions, including those caused by O_3 exposure. Several studies have shown that under abiotic stress, plant cells activate the alternative oxidase (AOX) pathway in their mitochondria, apart from the cytochrome (Cyt) pathway, which is the main mitochondrial electron transport chain (Vanlerberghe et al., 2013; Dinakar et al., 20160). This alternative AOX pathway features a cyanide-resistant ubiquinol oxidase located in the inner mitochondrial membrane, which facilitates the direct transfer of electrons from the ubiquinone pool to oxygen, circumventing the proton-pumping complexes III and IV. By circumventing Complex III and IV, AOX significantly diminishes ATP production, leading to the energy being transformed into heat (Li et al., 2024). Most importantly, AOX aids in preventing the overreduction of upstream electron-transport components, thereby decreasing ROS formation. Under stress conditions, this is of significant importance for the plant as it reduces further potential damage to cellular components, including the photosynthetic machinery (Manbir et al., 2022).

Anthocyanins, water-soluble pigments in plant cells, play a crucial role in alleviating photoinhibition due to their ability to absorb harmful UV radiation (280-315 nm), thus protecting intracellular components, including chloroplasts, from potential damage (Agati et al., 2021). They also possess strong antioxidant activities, preventing or reducing the damage caused by ROS. Anthocyanins exhibit their antioxidant effects mainly through hydrogen atom transfer (HAT) and single-electron transfer (SET) mechanisms. In the HAT mechanism, anthocyanin interacts with ROS by transferring one of its hydrogen atoms to the ROS through the homolytic cleavage of an -OH bond. In contrast, the SET mechanism involves the transfer of a single electron from the anthocyanin to the ROS, resulting in the ionization of both substances in the process (Sadowska-Bartosz & Bartosz, 2024).

Unlike anthocyanidins, the levels of chlorophyll and photosynthetic proteins significantly decrease under O_3 stress conditions, which in turn reduces photosynthetic capacity and efficiency, particularly in older leaves. This implies that the transcript levels of genes encoding proteins involved in the light-dependent reactions, the Calvin cycle, and pigment synthesis are significantly reduced under O_3 stress conditions (Han et al., 2023). Their reduction does not, however, necessarily translate to weakening the plant. Moreover, many scientists view a decline in the photosynthesis rate under stress conditions as a hidden cost of defense, as the plant reallocates its resources from growth to defense in order to overcome stressful conditions as quickly as possible (Huot et al., 2014; Serrano-Mislata et al., 2025; Zrimec et al., 2025). If this occurs, the plant increases the rate of photosynthesis to provide the resources necessary for its further growth and development.

Conversely, the genes involved in the signaling network and defense mechanisms against O_3 stress have different transcriptomic responses; their expression increases under O_3 stress (Ludwikow & Sadowski, 2008).

Modulation of antioxidant defense system

Plenty of studies have shown that O_3, after entering leaves, induces the accumulation of ROS in the apoplast through its conversion into superoxide anion radicals (O_2^-), hydrogen peroxide (H_2O_2), or singlet oxygen ($^1O_2$) upon interaction with water (Keutgen & Pawelzik, 2008; Vahisalu et al., 2010; Vaultier & Jolivet,

2015). ROS are well-known for their dual role in plants, functioning as both damaging and advantageous species (Panda et al., 2024). On the one hand, they are crucial in integrating external and intracellular signals, while also acting as critical regulators of plant growth and development. On the other hand, their overproduction at levels that go beyond the antioxidant scavenging capacity results in oxidative stress, recognized as a damaging process involved in the destruction of cell structures (Alam et al., 2025).

Antioxidant compounds in the apoplast serve as the initial defense against ROS, with ascorbate and glutathione being the main non-enzymatic ROS scavengers (Cannea & Padiglia, 2025). Piechowiak et al. (2026) reported that exposure of radish sprouts to O_3 stress resulted in a significant increase in ascorbate content by 14% and glutathione by 25% compared to the control. The observed increases in ascorbate and glutathione levels were associated with a heightened expression of proteins that play a role in the biosynthesis of these metabolites.

The ability of plants to neutralize O_3-induced ROS is not limited to only these two metabolites. The detoxification of ROS involves a sophisticated network that also includes various non-enzymatic antioxidants, such as tocopherols and flavonoids, along with enzymatic antioxidants (Hasanuzzaman et al., 2020). In this context, several studies have shown that under O_3 stress, plants are capable of enhancing their antioxidative systems by stimulating the gene expression and post-translational modifications of antioxidant enzymes such as superoxide dismutase (SOD), ascorbate peroxidase (APX), and catalase (CAT) (Mishra et al., 2023; Wang et al., 2023b; Jin et al., 2025). SOD catalyzes the dismutation of two molecules of O_2^- to less hazardous molecules: H_2O_2 and molecular oxygen (Rajput et al., 2021). H_2O_2 is extremely dangerous when present in high concentrations, as it converts into hydroxyl radicals, the most reactive and destructive ROS, which can cause irreversible damage to cellular structures. However, plant cells possess a strong antioxidant defense mechanism to counteract H_2O_2, with CAT and APX serving as the main enzymes for neutralizing H_2O_2 (Černý et al., 2018). CAT protects the cell against H_2O_2 by facilitating its breakdown into O_2 and H_2O, while APX decomposes H_2O_2 using ascorbate as an electron donor (Gomes et al., 2022). In general, the plant under O_3 exposure initiates numerous signaling pathways, all aimed at enhancing antioxidant capacity, either by producing enzymatic or non-enzymatic antioxidants or by generating metabolites that contribute to repairing damage caused by oxidative stress.

Secondary metabolism

In response to O_3 stress, the plant enhances the production of secondary metabolites, which are organic compounds that serve as a defense against both biotic and abiotic stresses. Guo et al. (2024) reported that O_3 exposure greatly increased the rate of carbon flux into secondary metabolic pathways, causing a change in resource allocation that affected the synthesis of secondary metabolites. All plants are able to produce secondary metabolites (SMs), especially under O_3 stress conditions, but this process exhibits remarkable genotypic variation and high phenotypic plasticity (Gu et al., 2025). SMs consist of a broad spectrum of compounds, featuring more than 12,000 alkaloids, 40,000 isoprenoids, and 8,000 phenylpropanoids, all of which are uniquely produced by plants (Elshafie et al., 2023). It is estimated that the total number of SMs surpasses 200,000; nonetheless, the actual figure is likely much greater (Nomura et al., 2018).

On the basis of their chemical structures, SMs can be broadly divided into three categories: terpenoids, phenolic compounds, and nitrogen-containing compounds. Among terpenoids, the most common compounds include sterols, carotenoids, saponins, and glycosides. In the category of phenolic compounds, flavonoids, phenolic acids, lignin, and tannins are prominent, while among nitrogen-containing compounds, alkaloids are the most represented (Jan et al., 2021).

Depending on their volatility, SMs in plants can be classified as either non-volatile or volatile. Volatile SMs are often characterized by a complex mixture of low-molecular-weight lipophilic compounds that mainly arise from terpenoid biosynthetic pathways, seemingly produced as a defense mechanism to prevent O_3

uptake. Volatile SMs also affect the interactions between plants and their habitats, playing a crucial role in coordinating plant-environment relationships (Abbas & Wang, 2025).

The phenylpropanoid, terpenoid, and alkaloid pathways represent the major metabolic pathways through which plant SMs are synthesized. Among these, the phenylpropanoid metabolic pathway is recognized as the most important secondary metabolic pathway associated with defense against abiotic stress, as it contributes directly or indirectly to the antioxidant defense systems in plants (Jangpangi et al., 2025). Some of the more significant end products of the phenylpropanoid pathway are flavonoids, hydroxycinnamic acid esters, and the precursors of lignin and tannins, all of which belong to phenolic compounds (Ninkuu et al., 2025). The importance of phenolic compounds lies not only in their ability to enhance the antioxidant capacity of the plant but also in their contribution to aesthetic quality parameters like color and taste, indicating their significant role in the adaptation of plants to the specific conditions of their native habitats (Kisiriko et al., 2021).

Alkaloids are another important class of plant SMs that play an important role in the plant's response to challenging living conditions, such as O_3 stress. O_3-induced alkaloid accumulation in plants has been documented in various studies, indicating that plants initiate alkaloid biosynthesis as a compensatory defense mechanism (Ansari et al., 2021; Pant et al., 2021; Ansari et al., 2023). Overall, alkaloids act as strong chemical deterrents, enhancing the plant's defense systems against environmental challenges. It is also important to note that certain SMs, including plant hormones JA, SA, and ET, serve as signaling molecules that help plants initiate signaling pathways aimed at producing substances that support their adaptation to unfavorable living conditions, particularly pronounced under O_3 stress.

CONCLUSIONS

O_3 pollution represents a significant global environmental issue, as its levels consistently rank among the most highly toxic air pollutants. Plants have evolved a complex set of defense mechanisms against O_3 stress, including O_3-induced stomatal regulation, photosynthetic adjustments, modulation of the antioxidant defense system, and secondary metabolism. In most plants, the first response to O_3 stress is stomatal closure, which takes place within a few minutes of O_3 exposure, consequently restricting O_3 uptake through the stomata. One negative outcome of this is the decreased influx of CO_2 into the leaves, resulting in a decline in photosynthetic rate. Additionally, O_3-induced ROS interfere with the photosynthetic electron transport chain, thereby further hindering the photosynthetic rate. However, plants possess inherent defense mechanisms that enable them to adjust photosynthesis to O_3 stress, including the regulation of the photosynthetic electron transport chain and an increase in anthocyanin production to protect the photosynthetic apparatus. Plants also possess various non-enzymatic and enzymatic antioxidants that assist in neutralizing the excessive production of ROS under O_3 stress conditions. A significant role in enhancing the plant's defense capacities against O_3 stress is played by numerous secondary metabolites that the plant intensively produces under such conditions. The value of these metabolites is twofold: they enhance the antioxidant capacity of the plant and serve as signaling molecules that facilitate the initiation of signaling pathways in plants aimed at producing substances that support the plant's adaptation to unfavorable living conditions.

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