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THE DUAL CHALLENGE OF CO_2 AND OZONE: INSIGHTS INTO PHOTOSYNTHESIS, VOC EMISSION AND BIOCHEMICAL RESPONSES

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Abstract

Human activities release various pollutants into the atmosphere, many of which directly affect plants. Among these pollutants are carbon dioxide (CO_2), which serves as the essential substrate for photosynthesis, and ozone (O_3), which acts as a harmful oxidant. With a particular emphasis on photosynthetic parameters, pigment content, volatile organic compound emissions, and biochemical features, this research investigates the responses of Raphanus sativus plants to increased exposure to CO_2 and O_3, focusing on three different varieties: Johanna, Helga, and Rozaria. To create conditions similar to those in the real world, the plants were grown under varying CO_2 concentrations (400, 800, and 1200 ppmv) and subjected to high ozone levels (100 ppb). Photosynthetic parameters were assessed through a gas exchange system, while volatile organic compound (VOC) emissions were analyzed using gas chromatography-mass spectrometry (GC-MS). Additionally, photosynthetic pigments were identified and quantified using the UHPLC-DAD system. Higher CO_2 levels initially enhanced net photosynthesis, but ozone severely reduced photosynthesis, leading to partial recovery after 24 hours. Ozone degraded chlorophyll a and b at all CO_2 concentrations, whereas zeaxanthin protected the photosynthetic system.

Key words*: abiotic stress, climate changes, ozone fumigation, secondary metabolites.*

INTRODUCTION

Atmospheric carbon dioxide (CO_2) levels continue to rise steadily, altering photosynthetic processes, carbon allocation, and physiological responses in terrestrial ecosystems. At the Mauna Loa Observatory, the annual mean CO_2 concentration is projected to increase by 2.37 ± 0.55 ppm in 2026 relative to 2025, reaching a record level of 429.4 ± 0.6 ppm.

Numerous studies show that higher CO_2 levels stimulate photosynthetic carbon assimilation and can also modify respiration, with robust responses reported in C_3 species (Leakey et al., 2006; Zheng et al., 2010; 2019; Ainsworth & Long, 2021; Li et al., 2023). However, the magnitude and persistence of this growth stimulation are highly context-dependent. In particular, plant responses to elevated CO_2 vary with nutrient supply, and the fertilization effect often weakens as nutrient availability declines (Menge & Field, 2007; Lenka & Lal, 2012; Pandey et al., 2015). As rising CO_2 can increase plant nutrient demand, nutrient limitation may therefore attenuate or even offset CO_2-driven gains in growth, especially under low-fertility conditions (Lenka & Lal, 2012; Pandey et al., 2015; Jin et al., 2025).

Tropospheric ozone (O_3) is a secondary pollutant formed through sunlight-driven photochemical reactions involving volatile organic compounds (VOCs) and nitrogen oxides (NO_x). It has been observed that free-tropospheric ozone levels have risen since the mid-1990s, with reported rates ranging from approximately 2% to 12% per decade, depending on the region. The biggest increases are usually seen in developing and quickly industrialising areas, such as East Asia, the Persian Gulf, India, northern South America, the Gulf of Guinea, and Malaysia/Indonesia. In Europe and North America, on the other hand, trends are usually

weaker and more mixed. The health effects of ozone exposure are most reliably recorded for the respiratory and cardiovascular systems (Kim et al., 2020). However, studies indicate potential links to respiratory mortality, the onset of asthma in children, and heightened respiratory symptoms in individuals with asthma (Kim et al., 2020; Hua et al., 2025).

Ozone primarily impacts above-ground plant tissues through direct leaf uptake, yet some of the earliest detectable responses can occur below ground (Nakadera et al., 2024). Root growth may be suppressed, respiratory costs can increase, and symbiotic interactions (e.g., with mycorrhizae) may be disturbed (Agathokleous et al., 2020; Zhang et al., 2024). With sufficiently high or prolonged exposure, ozone can reduce overall plant growth and alter typical plant-parasite relationships (Duque et al., 2019). Recent open-field enrichment experiments simulating future atmospheric conditions have emphasized the complex interplay between elevated carbon dioxide and tropospheric ozone in determining crop performance. In mustard (*Brassica juncea* L.), a major oilseed crop of economic and nutritional importance, elevated CO_2 (550 ppm) has been reported to enhance yield by stimulating photosynthesis and increasing photosynthate accumulation. In contrast, elevated ozone (65 ppb) significantly reduces yield by impairing branching patterns, biomass production, and seed formation. Importantly, when both factors co-occur, eCO_2 may partially mitigate ozone-induced yield losses, suggesting a buffering interaction under future climate scenarios characterized by rising atmospheric CO_2 and persistent ozone pollution. Moreover, varietal differences in responsiveness indicate that selecting ozone-tolerant and CO_2-responsive genotypes could be critical for sustaining mustard productivity under projected climate change conditions (JawaharJothi et al., 2025). Recent studies in wheat (*Triticum aestivum* L.) indicate that stomatal O_3 flux - a key determinant of ozone injury - varies substantially across different O_3 and CO_2 regimes and plays a central role in shaping physiological performance and yield. In two Indian wheat cultivars differing in O_3 sensitivity, elevated CO_2 reduced stomatal O_3 flux and partially mitigated O_3-induced yield losses. Notably, the O_3-sensitive cultivar exhibited greater yield protection under the combined eCO_2 + eO_3 treatment, likely due to enhanced allocation of photosynthates to reproductive structures, as reflected in a higher harvest index. Moreover, yield responses were more strongly correlated with stomatal O_3 flux in the sensitive cultivar than in the tolerant one, underscoring the importance of flux-based approaches for predicting crop performance under future atmospheric conditions (Mishra et al., 2024).

Given the concurrent rise in atmospheric CO_2 and tropospheric ozone under ongoing climate change, understanding their interactive effects on crop physiology is essential. Therefore, the present study aimed to evaluate how elevated CO_2 (800 and 1200 ppm) modulates ozone-induced stress (100 ppb) in three radish (*Raphanus sativus* L.) cultivars (Johanna, Helga, and Rozaria). We specifically assessed photosynthetic performance, chlorophyll content, and the accumulation of antioxidant-related secondary metabolites (total phenolics and flavonoids) to determine (i) whether elevated CO_2 mitigates ozone-induced physiological impairment and oxidative stress, and (ii) whether genotypic variability influences stress resilience under combined atmospheric conditions.

MATERIALS AND METHODS

The impact of increased CO_2 concentrations and ozone exposure on plant growth was studied by selecting and cultivating seeds from three *Raphanus sativus* (Brassicaceae) varieties. Those varieties included *Raphanus sativus* var. Johanna (Agrosel, Romania), *Raphanus sativus* var. Helga (Agrosel, Câmpia-Turzii, Romania) and *Raphanus sativus* var. Rozaria (Agrosel, Campia-Turzii, Romania).

A combination of commercial garden soil and sand was used to plant the seeds in 0.8-liter plastic containers. The plants were cultivated under artificial light from LED lamps at 800 $\mu mol\ m^{-2}s^{-1}$. We kept the daytime and nighttime temperatures at 25°C and 22°C, respectively, and the relative humidity at 65%. The light and dark cycles were set at 12 hours each. Every two days, the plants were watered until the soil was saturated. An ambient level of 400 ± 20 ppm CO_2 was used for plant cultivation, along with two higher levels of 800 and 1200 ppm CO_2,

respectively. Ozone gas at 100 ppb was used to fumigate the plants for 5 minutes.
The experiments were conducted on plants at least 4 weeks old, with at least 3 fully formed leaves throughout their growth cycle. The plants were fertilized with foliar fertilizers (Bionat Plus, Panetone SRL, Timisoara, Romania) and root fertilizers (Cropcare 11-11-21, YaraMila, Oslo, Norway).

Determination of photosynthetic parameters
A portable gas-exchange system (GFS-3000, Heinz Walz GmbH, Effeltrich, Germany) was employed to assess photosynthetic parameters, including CO_2 assimilation rate and stomatal conductance to water vapor. The device features an environment-controlled cuvette with an 8 cm^2 aperture and a complete-window leaf-chamber fluorimeter for sample illumination. A 4 cm^2 segment of radish leaf was positioned in the chamber for each measurement. All conditions remained constant except for CO_2, which was varied at 400, 800, and 1200 ppm during the experiment. The constant parameters were: air flow at 750 µmol s^{-1}, incident light at 1000 µmol m^{-2} s^{-1}, relative humidity at 65%, and cuvette temperature at 25 °C (Niinemets et al., 2010).

Chromatographic analysis of photosynthetic pigments
To identify and quantify photosynthetic pigments, a high-performance liquid chromatography (HPLC) system (NEXERA 8030, Shimadzu, Japan) in conjunction with a diode-array detector (DAD) was utilized following the procedures described in (Opriş et al., 2013).

Total Phenolic Content Determination
The extracts were obtained from fresh leaves using static maceration in a methanol-water mixture (60-40%) for 7 days at +4°C. All extracts were filtered using a 0.45 µm PTFE membrane. The total phenolic content of radish leaves, quantified as gallic acid equivalents (GAE), was assessed utilizing the Folin-Ciocalteu method as described (Lupitu et al., 2022).

Flavonoid Content Analysis
Total flavonoids were quantified by the $AlCl_3$ colorimetric method as described in our previous work (Copolovici et al., 2021), measuring absorbance at 434 nm and expressing results as rutin equivalents (calibration curve: 0.02-0.4 mg mL^{-1}).

Total Volatile Organic Compounds Determination
Total VOCs were collected and analyzed by GC–MS according to the protocol described in our previous study (Lupitu et al., 2025). Briefly, VOC emissions were sampled under the experimental treatments and quantified as the sum of identified compounds.

Statistical Analysis and Data Handling
All analyses were performed in triplicate, and results are presented as mean ± SD. Statistical significance was assessed by two-way ANOVA followed by Tukey's post hoc test using GraphPad Prism (v. 11.0.1), with $p < 0.05$ considered significant.

RESULTS AND DISCUSSIONS

Photosynthetic Parameters under Elevated CO_2 and Ozone Exposure
Figure 1a illustrates the effects of elevated carbon dioxide (800 and 1200 µmol mol^{-1}) and ozone exposure on the photosynthetic assimilation rate of the three radish cultivars (Johanna, Helga, and Rozaria). Under control conditions, assimilation rate increased progressively with rising CO_2 concentration in all cultivars, with the highest values recorded at 1200 µmol mol^{-1}, indicating strong CO_2 fertilization (Chen et al., 2022). Ozone exposure significantly reduced assimilation at all CO_2 levels, with the strongest inhibition observed at ambient CO_2.
However, increasing CO_2 partially alleviated ozone-induced suppression, particularly at 800 and 1200 µmol mol^{-1}, suggesting a protective interaction between elevated CO_2 and ozone stress. The same behaviour has been observed across different Indian mustard cultivars under strong CO_2 fertilization (Mishra et al., 2024). Across the three radish cultivars, both CO_2 concentration and ozone exposure had a significant effect on stomatal conductance (g_s) (Figure 1b).

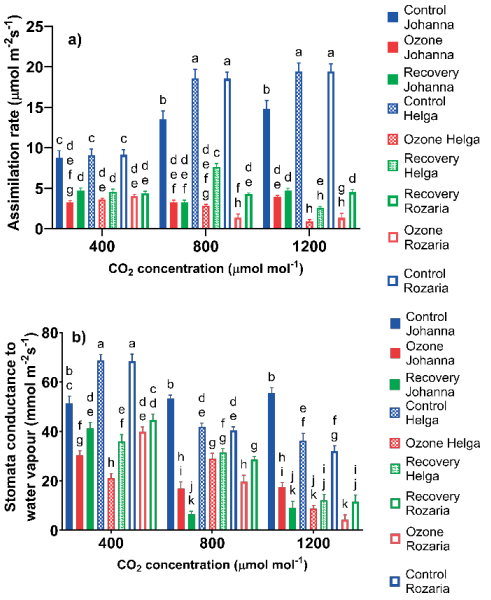


Figure 1. Effects of carbon dioxide (400, 800 and 1200 μmol mol^{-1}) and ozone exposure (100 ppb) on the net photosynthetic assimilation rate (μmol m^{-2} s^{-1}) (a) and stomatal conductance to water vapour (b) in three radish (*Raphanus sativus* L.) cultivars: Johanna, Helga, and Rozaria. Plants were subjected to control, ozone stress, and recovery treatments under each CO_2 concentration. Bars represent mean values ± SD. Different letters indicate statistically significant differences among treatments within each CO_2 level ($p < 0.05$)

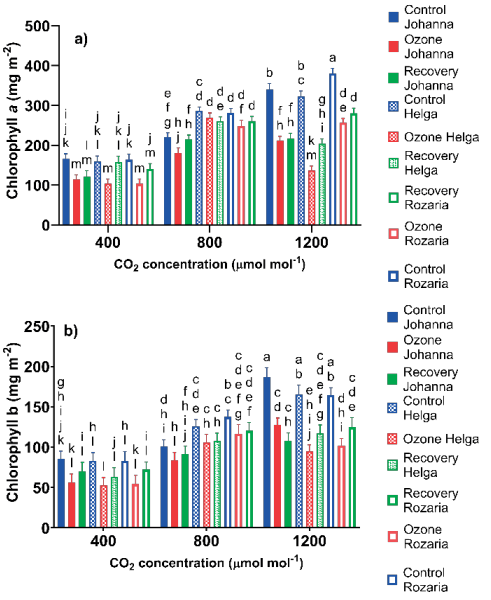


Figure 2. Effects of elevated CO_2 (400, 800 and 1200 μmol mol^{-1}) and ozone (100 ppb) on chlorophyll *a* (a) and chlorophyll *b* (b) content in three radish (*Raphanus sativus* L.) cultivars (Johanna, Helga, Rozaria). Plants were subjected to control, ozone stress, and recovery treatments under each CO_2 level. Bars represent mean ± SD. Different letters indicate significant differences among treatments within each CO_2 concentration ($p < 0.05$)

In controlled conditions, g_s decreased progressively with increasing CO_2 concentration, indicating partial stomatal closure in response to elevated CO_2 levels. A lot of research has shown that similar reactions occur when CO_2 levels rise (Ainsworth & Rogers, 2007; Franks et al., 2013; Ainsworth & Long, 2021), as elevated CO_2 typically triggers a reduction in stomatal aperture and conductance through both hydraulic and ABA-related signaling, resulting in lower g_s and reduced stomatal diffusion of gases (Xu et al., 2016). At higher CO_2 levels, the ozone-induced drops in g_s were less noticeable. It indicates that CO_2 enrichment altered stomatal responses and may have limited the amount of ozone they could take in (Bhatia et al., 2021).

Photosynthetic Pigment Responses

Chlorophyll content was significantly affected by both CO_2 concentration and ozone exposure in all three radish cultivars (Figure 2).

Under control conditions, chlorophyll *a* and chlorophyll *b* increased progressively with rising CO_2 levels, indicating enhanced photosynthetic capacity under CO_2 enrichment. The increase in chlorophyll content under elevated CO_2 may be linked to increased Rubisco carboxylation capacity, suggesting coordinated upregulation of the photosynthetic machinery under CO_2 enrichment (Wang et al., 2025).

Both chlorophyll fractions decreased significantly upon ozone exposure, especially at ambient CO_2 levels, indicating oxidative damage to the photosynthetic apparatus. However, the ozone-induced decrease in chlorophyll content was lessened under high CO_2, suggesting a buffering or protective effect of CO_2 enrichment (Férriz et al., 2025).

Among cultivars, Johanna and Helga generally maintained higher chlorophyll levels under combined treatments than Rozaria, which showed a more pronounced decline under ozone stress, especially at lower CO_2 concentrations.

Recovery treatments partially restored chlorophyll content, although values did not always reach control levels. It is still not clear whether the higher chlorophyll content is due to structural changes in the photosynthetic apparatus or to slower pigment breakdown. The interaction between increased carbon assimilation and modulation of oxidative stress is likely to affect the stability of photosynthetic pigments under multiple atmospheric stressors (Ainsworth & Rogers, 2007; Ainsworth & Long, 2021).

Antioxidant Compounds: Total Phenolics and Flavonoids

The total phenolic content was significantly influenced by both CO_2 concentration and ozone exposure among the three radish cultivars (Figure 3a).

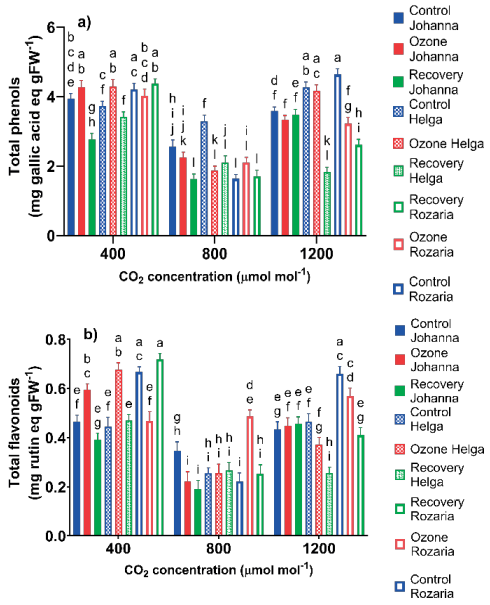


Figure 3. Effects of CO_2 concentration (400, 800 and 1200 µmol mol^{-1}) and ozone exposure (100 ppb) on (a) total phenolic content and (b) total flavonoid content in three radish (*Raphanus sativus* L.) cultivars (Johanna, Helga and Rozaria) under control, ozone and recovery treatments. Values are means ± SD (n = 3). Different letters indicate significant differences among treatments within each CO_2 level (two-way ANOVA followed by Tukey's test, $p < 0.05$)

Ozone treatment typically increased phenolic accumulation relative to control plants, especially under ambient carbon dioxide, suggesting the activation of antioxidant defense mechanisms in response to oxidative stress (Winyard et al., 2005).

Phenolic levels exhibited greater variability among cultivars under elevated CO_2 conditions. In some cases, CO_2 enrichment alone led to a marginal decrease in phenolic concentration compared to ambient conditions. Conversely, under the combined eCO_2 and eO_3 treatment, phenolic accumulation was consistently higher than in control plants, yet frequently lower than in conditions with ozone alone. This implies that increased CO_2 may partially influence ozone-induced oxidative stress responses (Bhatia et al., 2021). There were clear differences between cultivars. For example, Johanna showed the strongest increase in phenolics under ozone stress, while Rozaria showed a more moderate response.

The increase in total phenolics during ozone exposure indicates the activation of secondary metabolic pathways that are responsible for scavenging reactive oxygen species (ROS) (Jin et al., 2025). Phenolic compounds are important non-enzymatic antioxidants that help protect membranes and maintain the stability of the photosynthetic apparatus under high oxidative stress (Tamaoki, 2008; Piechowiak et al., 2026). The diminished phenolic response in elevated CO_2 conditions may indicate reduced oxidative stress, potentially resulting from decreased stomatal ozone absorption and enhanced carbon availability, which facilitate metabolic equilibrium. The interplay between carbon enrichment and ozone stress seems to govern the equilibrium between growth and defense allocation in radish cultivars.

For all three radish cultivars, CO_2 concentration and ozone exposure significantly affected total flavonoid content (Figure 3b). Compared with control plants, ozone treatment generally increased flavonoid accumulation, especially under ambient CO_2, suggesting that antioxidant defense mechanisms were activated in response to oxidative stress. At elevated CO_2 levels, flavonoid levels varied across cultivars. In some instances, CO_2 enrichment alone did not significantly enhance flavonoid content relative to ambient conditions; however, under the combined eCO_2 + eO_3 treatment, flavonoid accumulation persisted at elevated levels,

indicating that secondary metabolism remained active under stress.

Helga had the highest flavonoid levels when exposed to ozone, especially at 400 and 800 µmol mol^{-1} CO_2. Rozaria, on the other hand, had lower values when exposed to both stress treatments. Johanna's responses were in the middle. These results indicate that flavonoid biosynthesis represents an important component of the oxidative stress response in radish, and its modulation under elevated CO_2 suggests a complex balance between carbon availability and defense allocation. These findings demonstrate that flavonoid biosynthesis is a significant aspect of the oxidative stress response in plants, and its alteration in response to increased CO_2 indicates a complex equilibrium between carbon availability and defense distribution (Falcone Ferreyra et al., 2012; Ibrahim & Jaafar, 2012).

Volatile organic compound emissions

Ozone exposure significantly affected total VOC emissions, with clear patterns that depended on cultivar and CO_2 levels. Under controlled conditions, VOC emissions remained relatively low across all CO_2 levels (Figure 4). Conversely, ozone treatment resulted in a significant increase in total VOCs across all cultivars, consistent with the activation of stress-related volatile emission pathways under oxidative stress.

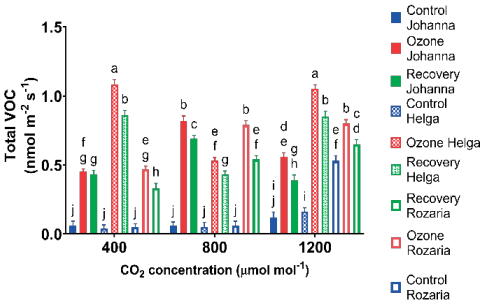


Figure 4. Effects of CO_2 concentration (400, 800 and 1200 µmol mol^{-1}) and ozone exposure (100 ppb) on total VOC emissions in three radish (*Raphanus sativus* L.) cultivars (Johanna, Helga and Rozaria) under control, ozone and recovery treatments. Values are means ± SD (n = 3). Different letters indicate significant differences among treatments within each CO_2 level (two-way ANOVA followed by Tukey's test, $p < 0.05$)

Higher levels of CO_2 altered VOC responses to ozone. At 800 and 1200 µmol mol^{-1} CO_2, VOC emissions under ozone differed from those under ambient CO_2. This suggests that the amount of carbon available and the way stomata function when CO_2 levels are high affect volatile release. Recovery treatments showed VOC levels midway between those of plants stressed by ozone, indicating that the plants partially recovered physiological status after the stress was removed, but differences between cultivars persisted. In general, the data show that total VOC emissions are a good indicator of ozone stress and that higher CO_2 levels can alter this response, with differences among Johanna, Helga, and Rozaria.

Total VOC emissions increased significantly in the presence of ozone, supporting the idea that O_3 is a strong oxidative stressor that triggers the release of stress-related volatiles used for defense and signaling (Li et al., 2017). The modulation of this response under elevated CO_2 suggests that the two atmospheric drivers do not exert simply additive effects, but rather interact in a more complex manner. This is in line with evidence that multiple concurrent stresses can significantly alter the size and composition of plant VOC emissions (Holopainen & Gershenzon, 2010). One possible explanation is that CO_2-Induced stomatal regulation reduces the amount of O_3 that stomata take in, thereby lowering oxidative pressure within the plant and partially blocking ozone-driven volatile signaling. However, changes in carbon availability under elevated CO_2 may still allow the formation of *de novo* VOCs (Himanen et al., 2009; Holopainen & Gershenzon, 2010).

CONCLUSIONS

Higher levels of CO_2 improved the physiological performance of radishes by increasing net CO_2 assimilation and raising the levels of chlorophyll a and b in all cultivars. This is consistent with a CO_2 fertilization response. On the other hand, exposure to 100 ppb of ozone clearly induced oxidative stress, lowering chlorophyll content and assimilation, and altering stomatal conductance. This showed that the photosynthetic machinery was not working properly.

Significantly, increased CO_2 levels (800-1200 ppm) partially alleviated ozone damage, as evidenced by a diminished ozone-induced reduction in assimilation, stomatal conductance, and pigment pools relative to ambient CO_2, indicating a buffering interaction among concurrent atmospheric change factors. Ozone also triggered secondary metabolism associated with antioxidants, as evidenced by higher levels of total phenolics and flavonoids. The fact that these levels changed when CO_2 levels rose suggests that the balance between growth and defence allocation is changing. Total VOC emissions rose sharply when ozone was present, and CO_2 levels also affected them. This shows that volatile release is a sensitive indicator of ozone stress, and its strength depends on how CO_2 affects stomatal regulation and carbon availability. Lastly, cultivar-specific response patterns (for example, Johanna had a stronger phenolic induction, Helga had a higher flavonoid accumulation, and Rozaria was generally more sensitive under combined stress) show that there is a lot of genotypic variability and support the idea that cultivar selection could help crops do well in the future when CO_2 levels are rising.

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