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Wheat (C3) and maize (C4) adaptive responses to soil thallium toxicity under elevated CO_2 conditions

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Abstract: This study investigated how wheat (C3) and maize (C4) respond to soil thallium (Tl) contamination and elevated CO_2 (eCO_2), aiming to understand strategies for mitigating oxidative stress. Under eCO_2, both crops showed higher biomass production. However, high Tl concentration (120 mg/kg) significantly decreased fresh and dry weights by 31–59%, which translated directly to compromised yield. This growth decline is linked to impaired photosynthesis, evidenced by a 54–57% drop in net photosynthetic rate under elevated Tl. Such photosynthetic inhibition intensifies oxidative stress, marked by increased membrane damage and hydrogen peroxide (H_2O_2). Furthermore, photorespiration contributed to oxidative stress by generating H_2O_2, with increased activities of glycolate oxidase and hydroxypyruvate reductase rising by 122% and 201%, in wheat and by 179% and 39% in maize, respectively, in response to 120 mg/kg TI under eCO_2 conditions. Simultaneously, to mitigate oxidative damage, antioxidant defences were significantly enhanced, resulting in increased activity of the ascorbate (ASC)/glutathione (GSH) cycle, along with elevated levels of metallothionein and phytochelatin for Tl sequestration, as well as augmented glutathione S-transferase activity. Overall, findings reveal complex interactions between CO_2 and Tl, highlighting species-specific adaptive responses of C3 and C4 plants. C3 plants use photorespiration to combat oxidative stress, while C3 and C4 plants have strong antioxidant systems to reduce the effects of oxidative stress, promoting crop resilience and growth despite Tl toxicity.

Keywords: climate changes; functional group; heavy metal; redox status; detoxification

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Maize (*Zea mays* L., a C4 species) and wheat (*Triticum aestivum* L., a C3 species) are key cereal crops that contribute significantly to global food security and economic stability (Grote et al. 2021). They contain important nutrients such as starch, carbohydrates, proteins, fats, vitamins, amino acids, and fatty acids, which are essential for overall well-being (Sahu et al. 2023). Additionally, these crops are rich in bioactive phytochemicals, particularly phenolic compounds, which possess health-beneficial properties and enhance their nutraceutical values (Patra et al. 2023). Phenolics and other phytochemicals like flavonoids and alkaloids are distributed in both free and bound forms within the grains, contributing to their positive effects on human health (Sahu et al. 2023). Despite their importance, the growth, yield, and long-term agricultural sustainability of wheat and maize are facing significant challenges due to climate change and soil contamination, particularly from salinity, heavy metals and toxic elements (Alotaibi et al. 2021, Mereu et al. 2021, Sheteiwy et al. 2022, Tao et al. 2022, El-Sawah et al. 2023, Wang et al. 2025). Thallium (Tl) is a toxic heavy metal often found in trace amounts in the environment due to industrial processes, mining activities, and the combustion of fossil fuels (Karbowska 2016). Its toxicity arises primarily from its chemical similarity to potassium (K), which can lead to Tl mistakenly being taken up by plants in place of K (Rodríguez-Mercado and Altamirano-Lozano 2013). This misuptake can disrupt essential physiological processes, resulting in reduced plant growth, impaired photosynthesis, and overall detrimental effects on crop health (Versieren et al. 2017, Shakoor et al. 2024). Understanding Tl's sources and toxic effects is critical for mitigating its impact on agricultural productivity and environmental health.

TI can accumulate in various regions worldwide, including parts of Europe and China (Xiao et al. 2004, Cabala and Teper 2007). Its plant uptake allows it to enter the food chain, posing significant toxicity risks, potentially greater than mercury and cadmium (Amin et al. 2013). High TI levels reduce plant growth and photosynthesis and cause pigment oxidation (Abdel-Mawgoud et al. 2023). TI may also disrupt sulfur-containing compounds by binding to sulfhydryl groups, affecting amino acid metabolism (Pavlíčková et al. 2006). TI accumulation varies with soil properties and plant species' adaptability (Jia et al. 2010). Overall, the accumulation of TI in various organisms underscores the potential risks associated with its presence in the environment.

On the other hand, carbon dioxide (CO_2) emissions are on the rise, driven by the growth of industrial activities, reliance on fossil fuels, conversion of natural ecosystems, and suboptimal agricultural and forestry practices (Anwar et al. 2020). This has led to an increase in CO_2 concentration from 280 μmol CO_2/mol during pre-industrial times to approximately 416 μmol CO_2/mol today, with projections suggesting levels may exceed 700 μmol CO_2/mol by the century's end (Naudts et al. 2013, Shabbaj et al. 2022). This increase in CO_2 is the foremost driver of climate change and global warming, contributing to more frequent and severe climate anomalies such as flooding, environmental stressors (like salinity, drought, and high temperatures), forest fires, heavy rainfall, and heat waves (Hagagy and AbdElgawad 2024a). Consequently, elevated CO_2 levels (eCO_2) are increasingly recognised as a significant factor influencing global agricultural output. Enhanced carbon availability affects various aspects of crop growth, including biomass production, photosynthesis, and metabolite profiles, even in plants grown under control conditions (AbdElgawad et al. 2022, Kaur et al. 2023, Hagagy and AbdElgawad 2024a).

The comparison of C3 and C4 plants in this study is underpinned by their fundamental differences in photosynthetic pathways, which significantly influence their responses to environmental stressors such as Tl toxicity and eCO_2 levels. While C3 and C4 plants exhibit distinct photosynthetic pathways adapted to their environments, these adaptations also influence their responses to elevated CO_2. C4 plants, like maize, utilise a more efficient photosynthetic mechanism under eCO_2 conditions, often resulting in greater biomass production compared to C3 species under similar conditions (Gowik and Westhoff 2011). Moreover, recent literature emphasises how wheat plants respond positively to elevated atmospheric CO_2, demonstrating improved photosynthetic capacity, reduced transpiration, and overall better productivity, which translates to higher grain yields (Alsherif et al. 2023). Previous studies have analysed field experiments on cereals grown in various environments, showcasing increased grain yield and its components at elevated CO_2 levels in non-stressed conditions. These findings suggest a more substantial rise in grain number per unit area compared to grain weight (Broberg et al. 2019, Blandino et al. 2020). Additionally, research highlights that the enhanced productivity of wheat in response to eCO_2 is linked to specific physiological mechanisms (Wang et al.

2013, Dubey et al. 2015), particularly the synthesis of bioactive compounds and antioxidant metabolites in non-stressed conditions (Blandino et al. 2020). Sreeharsha et al. (2019) noted that the availability of carbon under eCO_2 supports better plant growth by enhancing sink capacity and facilitating nitrogen assimilation. Furthermore, improvements in photosynthetic efficiency and photosystem-II performance under eCO_2 conditions have been documented, as indicated by increased chlorophyll fluorescence characteristics (Sekhar et al. 2015).

By elucidating the interactions between TI toxicity and eCO_2, this study aims to inform effective management strategies that can help mitigate environmental stressors and promote sustainable agricultural practices in response to climate change. This study is designed to explore the physiological, biochemical, and antioxidant responses of two crucial cereal crops, wheat and maize, when subjected to the combined stress of TI exposure and eCO_2 levels. The research will specifically evaluate how different concentrations of TI influence growth and the synthesis of bioactive compounds, while also examining the potential protective effects of eCO_2 against TI-induced stress. We hypothesise that increased CO_2 will mitigate some adverse physiological effects of TI stress by improving photosynthetic efficiency and enhancing antioxidant production in both crops, ultimately fostering better growth and yield.

MATERIAL AND METHODS

Plant materials and experimental setup. Uniform and healthy seeds of wheat (*Triticum aestivum* L. var. Giza 119) and maize (*Zea mays* L. var. Giza 2) were obtained from the Agricultural Research Centre in Giza, Egypt. The seeds were planted in pots containing a soil mixture of 70% sand and 30% Tref EGO substrates (Moerdijk, the Netherlands). A completely randomised design with three replicates was employed for the experiment, focusing on two key factors: varying levels of soil Tl contamination and different atmospheric CO_2 concentrations. The Tl concentrations used in this study were 0 mg/kg (control), 60 mg/kg, and 120 mg/kg, which were selected based on previous research indicating that cereal crops begin to exhibit significant negative growth effects at concentrations as low as 20 mg/kg, and critical toxicity thresholds were often observed between 50 mg/kg and 200 mg/kg (Abdel-Mawgoud et al. 2023, Hagagy and AbdElgawad 2024b). The soil was spiked with thallium$^{(I)}$ nitrate ($TlNO_3$) dissolved in water to achieve the target concentration of mg Tl per kg of soil. Therefore, the chosen levels not only encompass potential environmental contamination scenarios but also reflect realistic exposures that could occur in agricultural settings impacted by industrial activities and pollution. Concurrently, atmospheric CO_2 levels were set at 410 µmol CO_2/mol (control) and 710 µmol CO_2/mol (elevated levels), consistent with current and projected future climate conditions. Under high-emission scenarios (e.g., SSP5-8.5), CO_2 levels are projected to significantly exceed 550 ppm throughout the 21st century, reaching or surpassing 710 ppm around the 2060s or 2070s (IPPC 2021).

Furthermore, CO_2 was introduced into the chamber's airflow, and a CO_2 analyser (WMA-4, PP Systems, Hitchin, UK) was used to ensure maintenance of the desired CO_2 levels throughout the experiment. Specific temperature and light conditions were applied for optimal growth of wheat and maize seedlings in controlled-environment chambers over 6 weeks. Wheat seedlings were grown at 20–25 °C temperatures with 16 h of light daily and moderate light intensity of 250 $\mu mol/m^2/s$ of photosynthetic active radiation (PAR). Maize seedlings were grown at 25–30 °C with 16 h of daily light at a higher light intensity of 700 $\mu mol/m^2/s$ of PAR. Additionally, maintaining humidity levels of 60–70% and ensuring adequate air circulation were considered to prevent disease and facilitate healthy growth (Sheteiwy et al. 2023). Then, shoots were harvested, cleaned, and immediately weighed to determine both fresh weight (FW) and dry weight (DW). For the DW measurement, the fresh samples were placed in a drying oven set to 65 °C until they reached a constant weight over 48 h.

Quantification of TI in plant tissues and soil. The measurement of TI in plant shoot tissues and soil is achieved through inductively coupled plasma mass spectrometry (ICP-MS) (Cao et al. 2000). For plant tissues, samples were digested using a mixture of nitric acid and hydrogen peroxide to ensure complete dissolution of organic matter and facilitate the release of TI. Soil samples were similarly treated to extract TI, with additional steps such as drying and sieving to ensure homogeneity. The resulting solutions were then analysed to determine TI concentration.

Evaluation of photosynthesis and photorespiratory metrics. The chlorophyll and carotenoid levels were analysed in shoot samples using a spectrophotometric method based on the modified Porra technique (Yaghoubi et al. 2021). Absorbance readings were taken at specific wavelengths (665.2, 652.4, and 470 nm) using a Synergy Mx microplate reader (Biotek Instruments Inc., Vermont, USA) (Yaghoubi et al. 2019). The net photosynthetic rate (P_n) and stomatal conductance (g_s) were measured for the most recent fully developed leaves, specifically the third leaf from the apex, which is considered optimal for photosynthetic assessment in wheat and maize. This selection criterion was based on ensuring consistent physiological maturity and avoiding potential variations associated with younger or older leaves. Measurements were conducted using a LI-COR portable photosynthesis system (LI-COR 6400/XT, Lincoln, USA). A settling period of 30 min was implemented to allow for leaf acclimatisation. Light intensity was maintained at 800 µmol photons/m^2/s for wheat and 1 000 µmol photons/m^2/s for maize, accounting for their differing photosynthetic saturation points. Leaf temperature was consistently kept at 25 °C to ensure stable physiological responses during the measurement process. Reference CO_2 concentrations were set at 410 µmol CO_2/mol for the control treatment and 710 µmol CO_2/mol for the elevated treatment, ensuring accurate evaluation of the identified experimental objectives.

The maximum efficiency of photosystem II in dark-adapted leaves (F_v/F_m) was assessed with a Pulse Amplitude Modulated fluorometer (PAM–2500, Walz, Germany). In this context, F_m represents the maximum fluorescence and F_v denotes variable fluorescence, representing the difference between F_0 (the minimum fluorescence) and F_m (Lawson et al. 2002). To carry out the measurements, leaves were dark-adapted for 30 min using dark leaf clips (DLC-8). Following this, basal and maximum fluorescence were recorded in response to low-intensity red light (< 0.1 µmol photons/m^2/s) and a brief pulse of saturating white light (> 8 000 µmol photons/m^2/s) lasting 1 s (Yaghoubi et al. 2019).

The activity of glycolate oxidase (GO) was measured spectrophotometrically by observing the transformation of O-dianisidine into a coloured O-dianisidine radical cation (Kaundal et al. 2012). The analysis of hydroxypyruvate reductase (HPR) in leaf samples was conducted using NADH-HPR-NADH in conjunction with hydroxypyruvate (Bapatla et al. 2021).

Assessment of oxidative stress indicators. Malondialdehyde (MDA) levels in shoot tissues were determined by homogenising fresh samples in 80% ethanol and subjecting them to centrifugation at 7 000 g for 60 s with a MagNALyser. The resulting supernatant was then treated with thiobarbituric acid, forming a pinkish-red chromogen, with absorbance measured at 440, 532, and 600 nm (Hodges et al. 1999). Hydrogen peroxide (H_2O_2) concentration was assessed by employing a trichloroacetic acid solution along with assessing the peroxide-catalysed oxidation of Fe^{2+} (AbdElgawad et al. 2016). Additionally, the protein oxidation (PO) in leaf samples was quantified through the spectrophotometric determination of protein carbonyl content at a wavelength of 360 nm using a spectrophotometer (UV-2401 PC, Shimadzu, Tokyo, Japan) (Maiti et al. 2012).

Assessment of antioxidant enzyme activities. To evaluate antioxidant enzyme activities, shoot samples were first homogenised in a buffer solution composed of 50 mmol potassium phosphate (pH 7.0), 10% (*w*/*v*) polyvinyl pyrrolidone (PVP), 0.25% (*v/v*) Triton X-100, 1 mmol phenylmethylsulfonyl fluoride (PMSF), and 1 mmol ascorbate (ASC). The resulting mixture was then centrifuged to obtain a clear supernatant, which served as the basis for measuring the activity of various antioxidant enzymes (Hegab et al. 2008, Abdelaziz et al. 2022). The activity of superoxide dismutase (SOD) was determined through the inhibition of nitroblue tetrazolium (NBT) reduction, measured at 560 nm (Dhindsa et al. 1982). Peroxidase (POX) activity was assessed *via* the oxidation of pyrogallol, as detailed in the methodology by Kumar and Khan (1982). Catalase activity was quantified by monitoring the decomposition of H_2O_2 at a wavelength of 240 nm (Aebi 1984). The activities of ascorbate peroxidase (APX) and glutathione reductase (GR) were thoroughly described by Murshed et al. (2008). Monodehydroascorbate reductase (MDHAR) and dehydroascorbate reductase (DHAR) activities in shoot tissues were measured by evaluating the reduction of their respective substrates using a spectrophotometric method. Glutathione peroxidase (GPX) activity was measured based on decreased NADPH absorbance at 340 nm (Drotar et al. 1985).

Evaluation of antioxidant metabolite levels. The total antioxidant capacity (TAC) was assessed using the ferric-reducing antioxidant power (FRAP) method, employing Trolox as a standard reference (Selim et al. 2022). The concentrations of flavonoids and polyphenols were quantified through aluminium chloride calorimetric and Folin-Ciocalteu assays, following the protocols established by AbdElgawad et al. (2020) and Zhang et al. (2006), respectively. Additionally, tocopherol levels in the plant extracts

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were determined using high-performance liquid chromatography (HPLC) (Shimadzu, Hertogenbosch, the Netherlands), as per the methodology outlined by AbdElgawad et al. (2015), where dimethyl tocol (DMT) at a concentration of 5 ppm served as the internal standard. HPLC was also used to determine reduced glutathione (GSH) and ascorbate (ASC) levels (Hartley-Whitaker et al. 2001, Potters et al. 2004).

Evaluation of detoxification activities. Metallothioneins (MTC) and phytochelatins (PCs) in fresh shoot samples were quantified using HPLC combined with mass spectrometry (MS). The measurement of MTC was conducted through an enzyme-linked immunosorbent assay (ELISA) that detects specific antibodies (Palmiter 1998), while PCs were quantified by first derivatising the samples and then analysing them *via* HPLC-MS/MS (Cobbett and Goldsbrough 2002). Additionally, the overall activity of glutathione S-transferase (GST) was determined colourimetrically, utilising 1-chloro-2,4-dinitrobenzene (CDNB) as the substrate (Habig et al. 1974).

Statistical analysis. All statistical analyses were conducted using the SigmaPlot software (San Jose, USA). The study employed a completely randomised design with three biological replicates per treatment group. This included conducting a two-way analysis of variance (ANOVA), followed by Tukey's honestly significant difference (*HSD*) test for pairwise comparisons, and creating graphs to display the results visually. Results are shown as mean ± standard deviation. A significance level (α) of 0.05 was set for the Tukey's test.

RESULTS

TI content in plant and soil. We measured TI accumulation in plants at harvest to investigate if TI buildup in plant shoots contributes to growth reduction (Figure 1). The results indicated that both crops showed increased TI uptake with higher soil contamination levels and that aCO_2 conditions favoured greater TI accumulation in wheat and maize than eCO_2 (Figure 1). In wheat, eCO_2 conditions resulted in a 60% increase in tissue TI content at 120 mg/kg TI compared to 60 mg/kg. In comparison, aCO_2 conditions also led to a lesser increase of 43% at the same higher contamination level, with aCO_2 facilitating higher TI accumulation than eCO_2 at 120 mg/kg. In maize, the trend mirrored that of wheat; eCO_2 resulted in a 66% increase in TI content at 120 mg/kg *versus* 60 mg/kg, while aCO_2 showed a 55% increase under the same conditions, again highlighting higher TI accumulation in aCO_2 compared to eCO_2 at the higher TI concentration.

Plant biomass. TI accumulation reduced wheat and maize biomass under TI contamination conditions (Figure 2). On the other hand, eCO_2 led to significantly greater biomass when compared to aCO_2 across the various treatments (Figure 2). The highest biomass values were consistently found in eCO_2 treatments, while biomass diminished drastically with increased TI contamination, particularly highlighted by the stark contrast between the control and the contaminated treatments. In detail, the FW and DW of wheat plants were significantly influenced by the

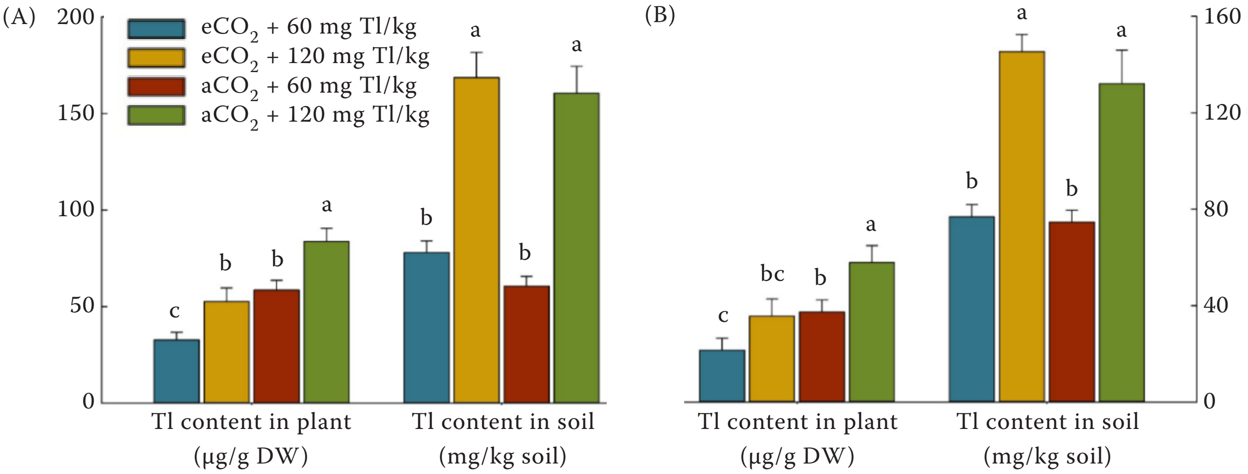

Figure 1. Thallium (TI) content in soil, (A) wheat and (B) maize in response to elevated CO_2 (eCO_2) and ambient CO_2 (aCO_2) conditions under different levels of soil TI contamination. The means in each parameter with similar small letter(s) are not significantly different at 5% probability level (Tukey's *HSD* (honestly significant difference) test). DW – dry weight

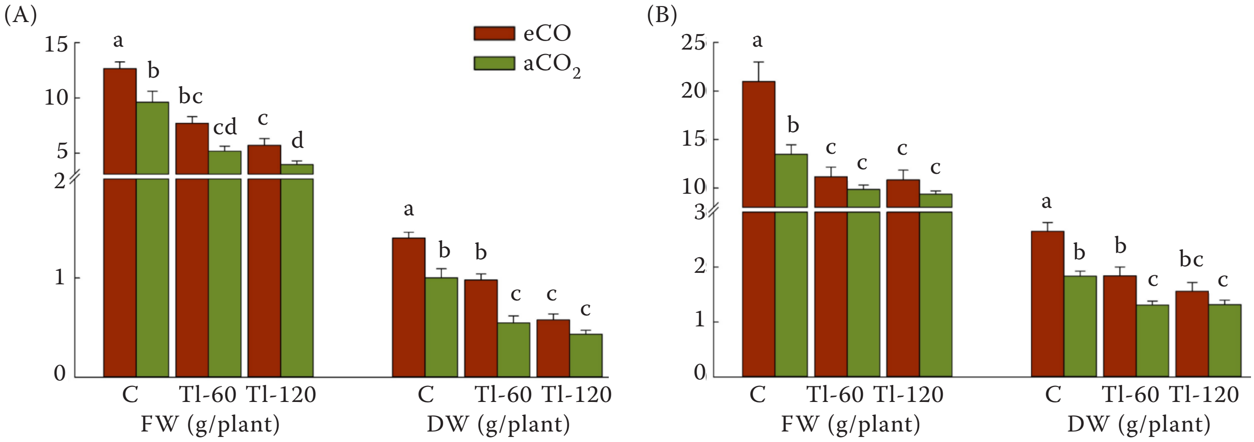

Figure 2. The effect of elevated CO_2 (eCO_2) and ambient CO_2 (aCO_2) conditions on plant biomass in (A) wheat and (B) maize under different levels of soil thallium (TI) contamination. The means in each parameter with similar small letter(s) are not significantly different at 5% probability level (Tukey's *HSD* (honestly significant difference) test). C – control; Tl-60 – 60 mg Tl/kg; Tl-120 – 120 mg Tl/kg

CO_2 and TI treatments. Under eCO_2 conditions, the wheat biomass was highest, with a considerable reduction observed when TI was added to the soil, particularly at 120 mg/kg TI, resulting in a decrease of 55% in FW and 59% in DW ($P < 0.05$). Adding 60 and 120 mg/kg TI for maize resulted in a decline to

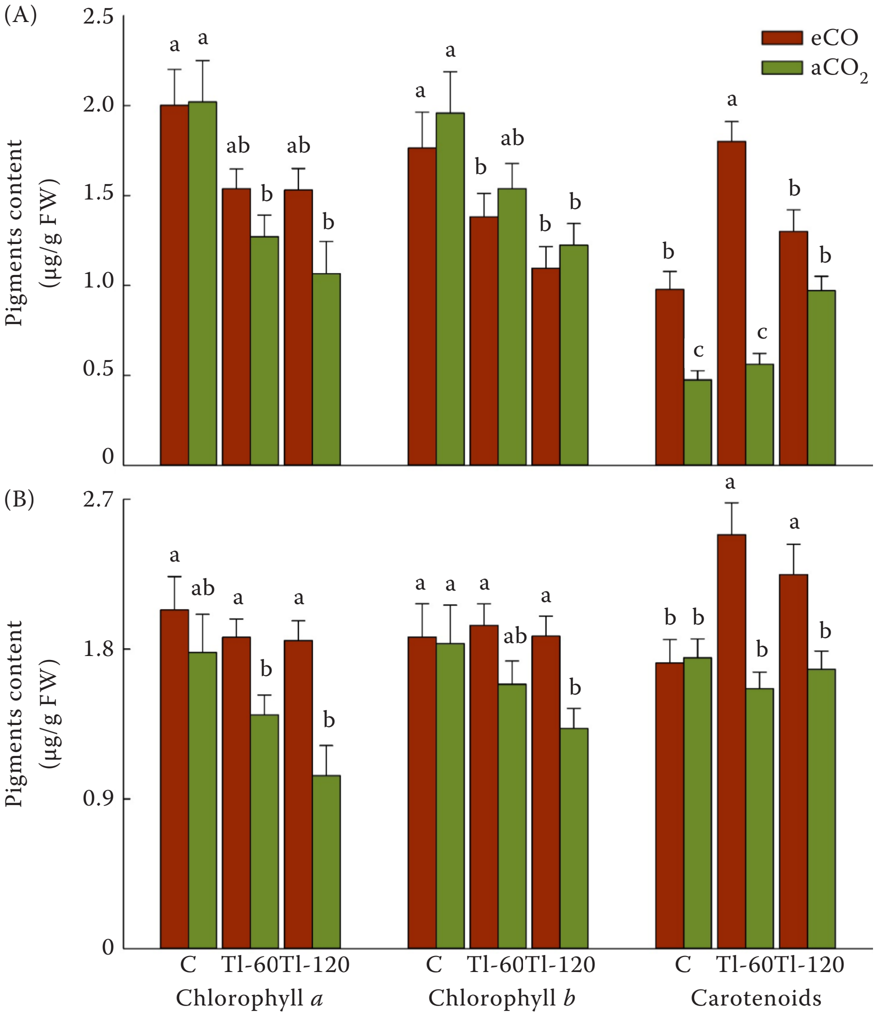

Figure 3. The effect of elevated CO_2 (eCO_2) and ambient CO_2 (aCO_2) conditions on photosynthetic pigments in (A) wheat and (B) maize under different levels of soil thallium (TI) contamination. The means in each parameter with similar small letter(s) are not significantly different at 5% probability level (Tukey's *HSD* (honestly significant difference) test). C – control; Tl-60 – 60 mg Tl/kg; Tl-120 – 120 mg Tl/kg

47% and 49% for FW and a decrease of 31% and 41% for DW, respectively ($P < 0.05$).

Photosynthetic parameters. Following the finding of diverse biomass productions in plants under varying CO_2 and soil TI levels, we studied the photosynthetic parameters for further understanding how these environmental changes affect plant health and productivity. Assessing changes in chlorophyll *a* (Chl *a*), chlorophyll *b* (Chl *b*), and carotenoids allows for the assessment of the effects of treatments on plant photosynthetic efficiency. The results showed that TI contamination adversely impacts pigment accumulation, especially in wheat, while maize shows some resilience (Figure 3). In wheat, the highest Chl *a* and Chl *b* levels occurred under aCO_2 and eCO_2 without TI contamination, while TI negatively affected pigment production. Carotenoids peaked under eCO_2, decreasing significantly with 120 mg/kg TI under aCO_2 (51% drop, $P < 0.05$). In maize, Chl *a* and Chl *b* were unaffected by TI under eCO_2 but decreased under aCO_2. Carotenoid levels were highest with 60 mg/kg TI under eCO_2 but fell under aCO_2 treatments (37% decrease with 60 mg/kg TI and 33% with 120 mg/kg TI).

Moreover, both plants exhibited significant declines in photosynthetic traits across different CO_2 levels and TI contamination (Figures 3–4). The highest P_n and g_s in both plants were observed under eCO_2 without TI, while the lowest were seen with aCO_2 and 120 mg/kg of TI, marking a significant difference ($P < 0.05$). Under eCO_2 conditions, P_n in wheat decreased by 26% and 54% when 60 and 120 mg/kg of TI were added, respectively, compared to eCO_2 alone ($P < 0.05$). In aCO_2 conditions, adding 60 mg/kg

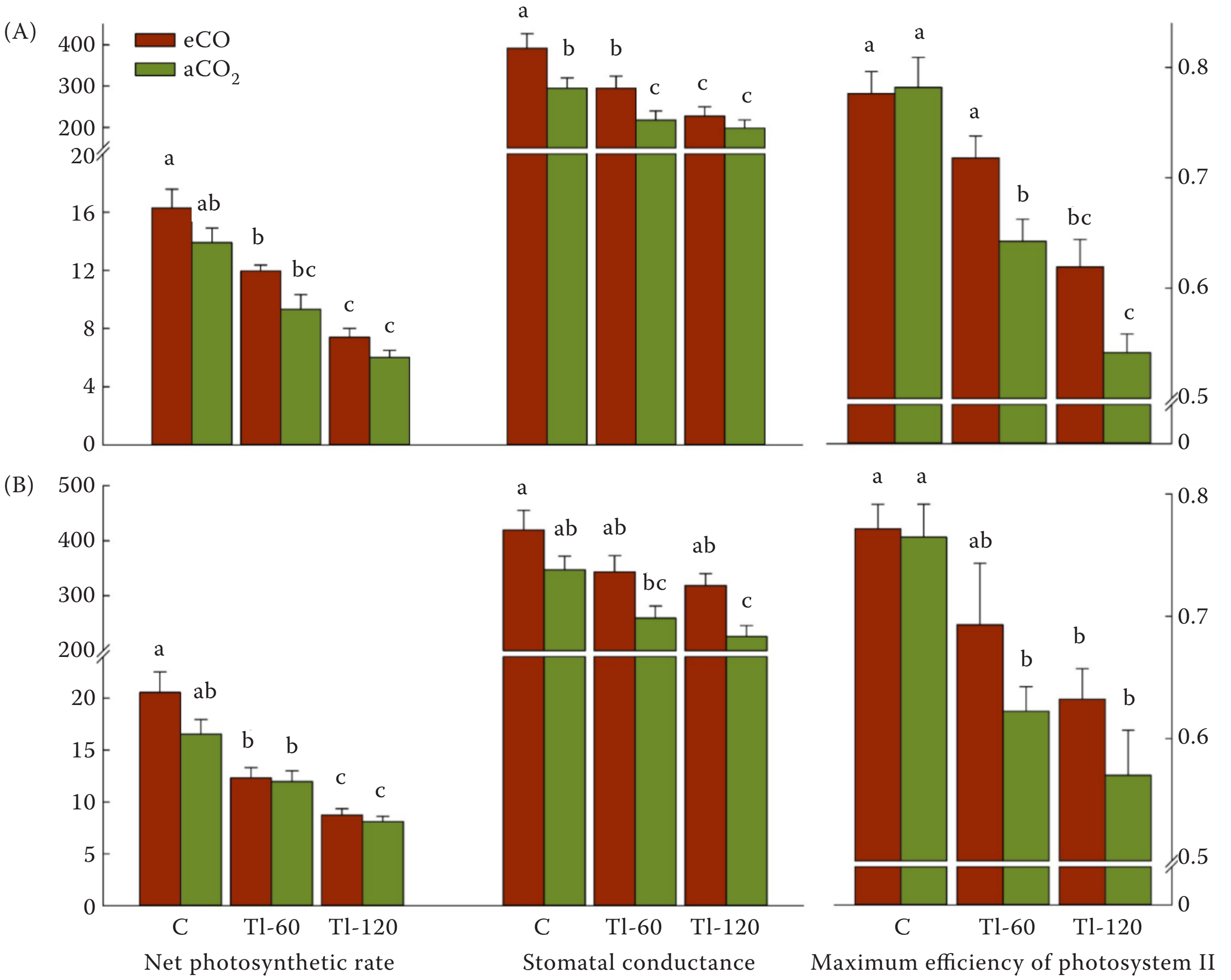

Figure 4. The effect of elevated CO_2 (eCO_2) and ambient CO_2 (aCO_2) conditions on photosynthetic parameters in (A) wheat and (B) maize under different levels of soil thallium (TI) contamination. The means in each parameter with similar small letter(s) are not significantly different at 5% probability level (Tukey's *HSD* (honestly significant difference) test). C – control; Tl-60 – 60 mg Tl/kg; Tl-120 – 120 mg Tl/kg

of TI reduced P_n by 44%, while 120 mg/kg of TI resulted in a striking 64% decrease compared to aCO_2 alone ($P < 0.05$). For g_s, wheat under eCO_2 displayed a 30% and 62% decline with 60 and 120 mg/kg TI, respectively, compared to eCO_2 alone ($P < 0.05$). These reductions in aCO_2 conditions were about 25% and 43% compared to aCO_2 alone ($P < 0.05$).

Photochemical efficiency of photosystem II, as indicated by F_v/F_m, decreased 8% ($P \geq 0.05$) with 60 mg/kg TI and by 20% ($P < 0.05$) with 120 mg/kg TI under eCO_2 conditions. Conversely, under aCO_2 conditions, F_v/F_m values dropped by 18% and 31% with 60 and 120 mg/kg TI, respectively ($P < 0.05$). The highest F_v/F_m in both plants was recorded in eCO_2 without TI, while the lowest was in aCO_2 with 120 mg/kg TI.

A similar trend was observed in maize, in which P_n dropped by 40% and 57% with 60 and 120 mg/kg TI, respectively, under eCO_2 compared to eCO_2 alone ($P < 0.05$). Similar reductions were found under aCO_2 by 28% ($P \geq 0.05$) and by 51% ($P < 0.05$) with 60 and 120 mg/kg TI, respectively, compared to aCO_2 alone. For g_s, only 120 mg/kg of TI resulted in a significant decrease in maize under both eCO_2 and aCO_2 conditions, being approximately 58% and 35% lower than the levels of eCO_2 and aCO_2 alone, respectively ($P < 0.05$). F_v/F_m in maize also reflected these patterns, showing a significant decrease of 18% with 120 mg/kg TI under eCO_2 conditions ($P < 0.05$). In aCO_2 conditions, F_v/F_m dropped by 19% and 26% with 60 and 120 mg/kg TI, respectively, compared to aCO_2 ($P < 0.05$) (Figure 4).

Photorespiratory metabolism. When comparing the impacts of CO_2 levels and TI contamination across both crops, it is evident that higher TI levels consistently lead to increased Gly/Ser ratios and GO and HPR activities, especially under aCO_2 conditions (Figure 5). The maximum responses under TI 120 mg/kg treatments were significantly greater than those

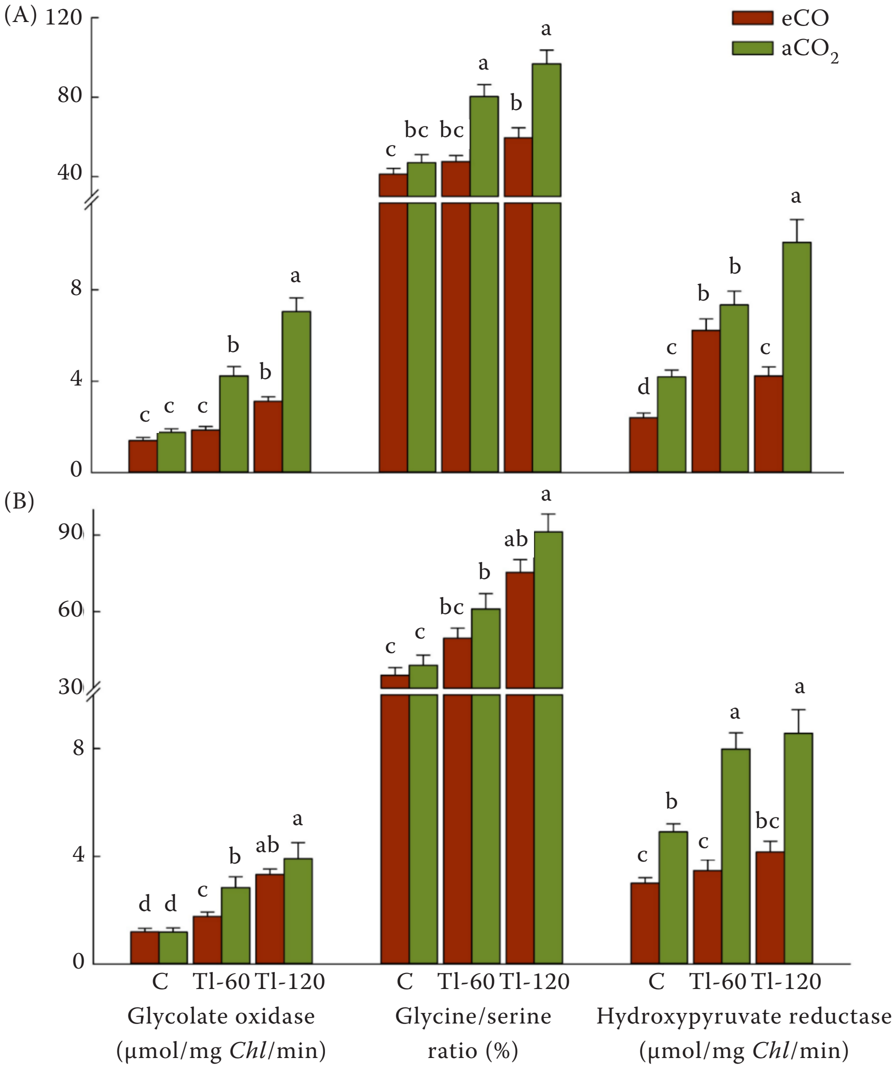

Figure 5. The effect of elevated CO_2 (eCO_2) and ambient CO_2 (aCO_2) conditions on photorespiratory metabolism in (A) wheat and (B) maize under different levels of soil thallium (TI) contamination. The means in each parameter with similar small letter(s) are not significantly different at 5% probability level (Tukey's *HSD* (honestly significant difference) test). C – control; Tl-60 – 60 mg Tl/kg; Tl-120 – 120 mg Tl/kg; *Chl* – chlorophyll

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seen in the controls, underscoring the interactive effects of CO_2 and Tl on photorespiratory processes in both wheat and maize. In wheat, the Gly/Ser ratio increased from 15% ($P \geq 0.05$) to 44% ($P < 0.05$) with Tl contamination under eCO_2, while under aCO_2, it rose from 71% to 106% under the same Tl treatments ($P < 0.05$). HPR and GO activities in wheat showed an increase of 159% and 32% to 201% and 122% with Tl under eCO_2, and a rise of 75% and 140% to 141% and 300% under aCO_2 conditions, respectively ($P < 0.05$). In maize, the Gly/Ser ratio in response to Tl treatments increased from 41% and 57% to 115% and 134% under eCO_2 and aCO_2, respectively ($P < 0.05$). Similarly, HPR and GO activities under eCO_2 increased from 16% ($P \geq 0.05$) and 49% to 39% and 179% ($P < 0.05$) in response to 60 and 120 mg/kg Tl, respectively, while they increased from 63% and 140% to 75% and 231% under aCO_2 ($P < 0.05$).

Oxidative markers content. Investigating oxidative markers is essential for assessing the oxidative stress that plants experience under varying environmental conditions, including eCO_2 and soil contamination with Tl. Based on the results, while both wheat and maize showed increased oxidative markers content with Tl contamination, aCO_2 conditions consistently resulted in higher stress responses than eCO_2 for both species (Figure 6), underscoring the adverse effects of Tl on plant health. In this regard, H_2O_2, MDA, and PO levels in wheat plants demonstrated a significant increase of 114, 78, and 77% under aCO_2 with 120 mg/kg Tl contamination compared to the same Tl level under eCO_2, respectively ($P < 0.05$). In maize, H_2O_2 levels increased by 131% under aCO_2 with 120 mg Tl compared to aCO_2 alone, surpassing the 35% increase seen under eCO_2 at the same Tl level ($P < 0.05$). Similarly, MDA levels in maize increased in both eCO_2 and aCO_2 conditions in response to Tl contamination, while increasing the PO levels were significant only under aCO_2 conditions ($P < 0.05$).

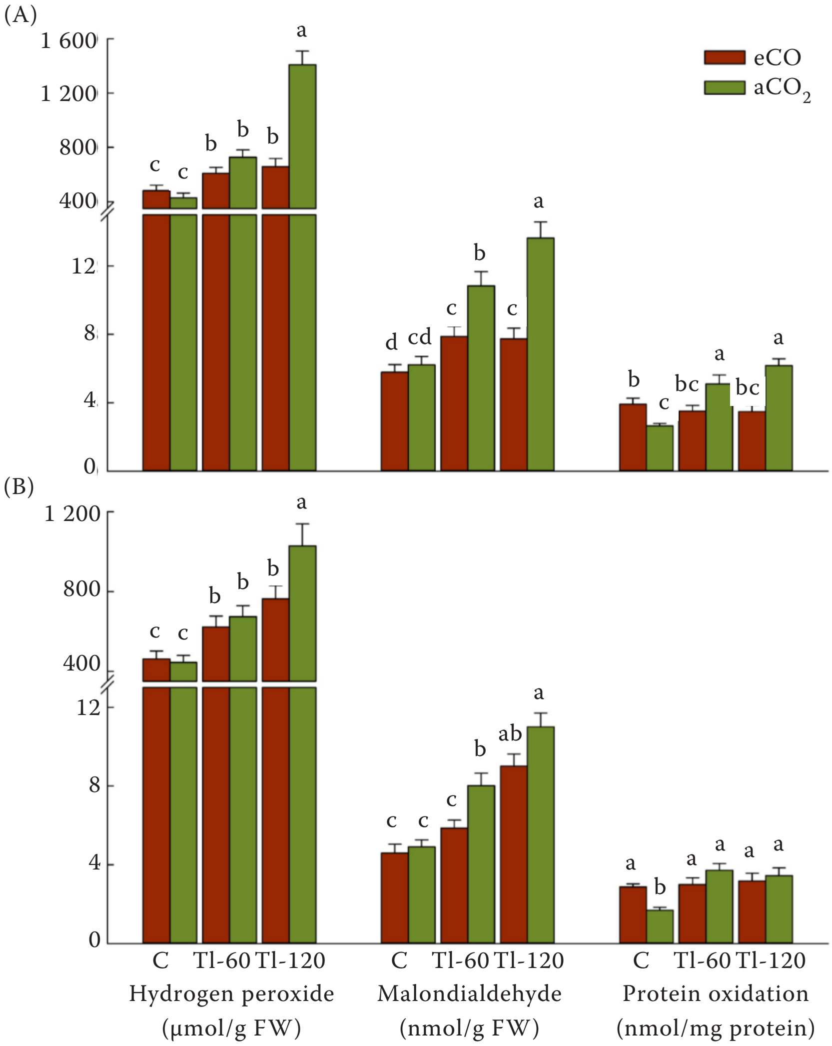

Figure 6. The effect of elevated CO_2 (eCO_2) and ambient CO_2 (aCO_2) conditions on the oxidative markers in (A) wheat and (B) maize under different levels of soil thallium (Tl) contamination. The means in each parameter with similar small letter(s) are not significantly different at 5% probability level (Tukey's *HSD* (honestly significant difference) test). C – control; Tl-60 – 60 mg Tl/kg; Tl-120 – 120 mg Tl/kg; FW – fresh weight

Total antioxidant capacity, non-enzymatic and enzymatic antioxidants. Investigating non-enzymatic and enzymatic antioxidants is crucial as these components highlight the plant's ability to counteract oxidative stress resulting from environmental factors. Almost all antioxidant parameters were significantly increased in both plants in response to increasing TI contamination, in some of which aCO_2 conditions generally elicited a stronger antioxidant response compared to eCO_2 (Tables 1 and 2). The increases observed in TAC, polyphenols, flavonoids, and various enzymatic antioxidants highlight the plants' adaptive strategies to combat oxidative stress induced by TI contamination. In this regard, TAC significantly increased at 120 mg/kg TI level in wheat plants under eCO_2, while under aCO_2, TAC showed a more pronounced overall increase in response to both TI levels, with differences of up to 58% at 120 mg/kg TI level ($P < 0.05$). Total polyphenol content showed a marked increase under both CO_2 conditions, with aCO_2 leading to a substantially greater enhancement compared to eCO_2, tracking changes of over 47% at 120 mg/kg TI ($P < 0.05$).

Flavonoid and total tocopherols content indicated a significantly greater increase under aCO_2 in response to different TI levels, underlining the effectiveness of this condition in promoting antioxidant levels. Moreover, the activity of the enzymatic antioxidants in wheat plants at a 60 mg/kg contamination level did not show a clear trend compared to the control. However almost all of them were significantly more active than the control at 120 mg/kg level under both eCO_2 and aCO_2 conditions by approximately 67% and 76% for POX, 39% and 58% for CAT, 42% and 52% for APX, 85% and 275% for DHAR, and 112% and 141% for GR, respectively ($P < 0.05$) (Table 1).

In maize, the trends in TAC and antioxidant compounds mirrored those seen in wheat with eCO_2, demonstrating a significant increase in TAC under both TI contamination levels. However, aCO_2 levels led to a considerably greater increase compared to the control, but only at the 120 mg/kg TI level. Also, the highest content of total polyphenols, flavonoids, total tocopherols, ASC, and GSH were obtained in plants grown at 120 mg/kg TI under both CO_2 conditions, with a marked increases of 92, 164, 51, 47, and 115% under eCO_2, and 196, 274, 125, 96, and 103% under aCO_2, compared to eCO_2 and aCO_2 alone, respectively ($P < 0.05$). Like wheat, the enzymatic antioxidant activity in maize plants at a contamination

Table 1. The effect of elevated CO_2 (eCO_2) and ambient CO_2 (aCO_2) conditions on total antioxidant capacity, non-enzymatic and enzymatic antioxidants in wheat plants under different levels of soil thallium (TI) contamination

Parameter	eCO_2			aCO_2		
	control	TI (60 mg)	TI (120 mg)	control	TI (60 mg)	TI (120 mg)
TAC (µmol Trolox/g FW)	25.92^{c}	30.21^{bc}	32.05^{b}	24.39^{c}	35.54^{b}	50.71^{a}
Polyphenols (mg GAE/g FW)	1.76^{bc}	2.66^{ab}	2.70^{ab}	1.46^{c}	2.19^{b}	3.97^{a}
Flavonoids (mg QE/g FW)	1.02^{bc}	1.17^{b}	1.31^{b}	0.78^{c}	1.35^{b}	2.02^{a}
ASC (µmol/g FW)	0.85^{c}	1.48^{b}	1.41^{b}	0.91^{c}	1.34^{b}	1.94^{a}
GSH (µmol/g FW)	0.39^{b}	0.45^{b}	0.41^{b}	0.40^{b}	0.51^{b}	0.71^{a}
Tocopherols (ng/g DW)	21.52^{bc}	24.35^{bc}	24.87^{bc}	20.99^{c}	25.82^{b}	36.96^{a}
POX (µmol/min/mg Pr)	1.06^{b}	2.11^{a}	1.77^{a}	0.96^{b}	1.00^{b}	1.70^{a}
CAT (µmol/min/mg Pr)	7.13^{bc}	11.53^{a}	9.94^{ab}	5.32^{c}	10.56^{ab}	8.43^{b}
SOD (µmol/min/mg Pr)	16.98^{b}	22.11^{ab}	18.97^{b}	18.54^{b}	18.83^{b}	26.85^{a}
APX (µmol/min/mg Pr)	0.27^{c}	1.07^{a}	0.66^{b}	0.35^{c}	0.51^{bc}	0.89^{a}
DHAR (µmol/min/mg Pr)	0.14^{c}	0.30^{ab}	0.25^{b}	0.11^{c}	0.25^{b}	0.41^{a}
MDHAR (µmol/min/mg Pr)	0.49^{b}	0.78^{a}	0.50^{b}	0.41^{bc}	0.35^{c}	0.41^{bc}
GR (µmol/min/mg Pr)	0.10^{b}	0.20^{a}	0.22^{a}	0.10^{b}	0.12^{b}	0.24^{a}
GPX (µmol/min/mg Pr)	0.61^{a}	0.60^{a}	0.59^{a}	0.34^{b}	0.70^{a}	0.61^{a}

At a 5% probability level, the Tukey *HSD* test reveals that means sharing the same letter(s) are not significantly distinct. TAC – total antioxidant capacity; ASC – ascorbate; GSH – glutathione; POX – peroxidase; CAT – catalase; SOD – superoxide dismutase; APX – ascorbate peroxidase; DHAR – dehydroascorbate reductase; MDHAR – monodehydroascorbate reductase; GR – glutathione reductase; GPX – glutathione peroxidase; FW – fresh weight; GAE – gallic acid; QE – quercetin; DW – dry weight

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Table 2. The effect of elevated CO_2 (eCO_2) and ambient CO_2 (aCO_2) conditions on total antioxidant capacity, non-enzymatic and enzymatic antioxidants in maize plants under different levels of soil thallium (TI) contamination

Parameter	eCO_2			aCO_2		
	control	TI (60 mg)	TI (120 mg)	control	TI (60 mg)	TI (120 mg)
TAC (µmol Trolox/g FW)	28.02^{c}	35.73^{ab}	39.43^{ab}	26.26^{c}	31.42^{bc}	42.89^{a}
Polyphenols (mg GAE/g FW)	1.95^{c}	2.86^{b}	3.75^{b}	1.64^{c}	3.59^{b}	4.86^{a}
Flavonoids (mg QE/g FW)	1.05^{c}	2.10^{b}	2.77^{ab}	0.82^{c}	1.96^{b}	3.09^{a}
ASC (µmol/g FW)	1.96^{c}	2.19^{bc}	2.89^{b}	1.83^{c}	2.29^{bc}	3.60^{a}
GSH (µmol/g FW)	0.32^{c}	0.56^{ab}	0.68^{a}	0.28^{c}	0.41^{bc}	0.54^{b}
Tocopherols (ng/g DW)	19.86^{b}	20.94^{b}	29.90^{a}	12.48^{c}	18.48^{b}	28.03^{a}
POX (µmol/min/mg Pr)	0.88^{c}	1.63^{b}	2.95^{a}	0.87^{c}	1.17^{bc}	1.62^{b}
CAT (µmol/min/mg Pr)	6.40^{bc}	9.36^{b}	15.67^{a}	4.81^{c}	8.76^{b}	13.69^{a}
SOD (µmol/min/mg Pr)	88.22^{bc}	89.68^{bc}	150.70^{a}	63.76^{c}	106.03^{b}	160.31^{a}
APX (µmol/min/mg Pr)	0.19^{d}	0.36^{c}	0.93^{a}	0.18^{d}	0.34^{c}	0.68^{b}
DHAR (µmol/min/mg Pr)	0.09^{c}	0.13^{bc}	0.19^{a}	0.09^{c}	0.10^{bc}	0.14^{b}
MDHAR (µmol/min/mg Pr)	0.53^{b}	0.43^{b}	0.82^{a}	0.36^{b}	0.36^{b}	0.47^{b}
GR (µmol/min/mg Pr)	0.12^{c}	0.33^{b}	0.56^{a}	0.12^{c}	0.33^{b}	0.48^{ab}
GPX (µmol/min/mg Pr)	0.31^{b}	0.50^{a}	0.53^{a}	0.24^{b}	0.51^{a}	0.55^{a}

At a 5% probability level, the Tukey *HSD* test reveals that means sharing the same letter(s) are not significantly distinct. TAC – total antioxidant capacity; ASC – ascorbate; GSH – glutathione; POX – peroxidase; CAT – catalase; SOD – superoxide dismutase; APX – ascorbate peroxidase; DHAR – dehydroascorbate reductase; MDHAR – monodehydroascorbate reductase; GR – glutathione reductase; GPX – glutathione peroxidase; FW – fresh weight; DW – dry weight; GAE – gallic acid; QE – quercetin; Pr – protein

level of 60 mg/kg TI did not show a discernible trend compared to the control. However, at the 120 mg/kg TI level, all measured antioxidant enzymes showed significant increases in activity under both CO_2 levels (except for MDHAR under aCO_2) compared to the control. Specifically, the observed increases under eCO_2 and aCO_2 in response to 120 mg/kg TI were approximately 236% and 86% for POX, 145% and 184% for CAT, 71% and 151% for SOD, 379% and 271% for APX, 108% and 58% for DHAR, 56% and 32% for MDHAR, 372% and 298% for GR, and 73% and 127% for GPX compared to the control, respectively (Table 2).

Detoxification activity. Both wheat and maize demonstrated a clear trend of increased detoxification activity with TI contamination under eCO_2 and aCO_2 (Figure 7). The most significant enhancements were noted at the highest level of TI contamination (120 mg/kg), indicating that both plants could effectively mitigate TI stress. Under eCO_2 conditions, MTC levels increased considerably in response to TI contamination, showing a notable increase (+77%) at 120 mg/kg TI contamination compared to control conditions ($P < 0.05$). Similarly, phytochelatin levels under eCO_2 with 120 mg/kg TI contamination experienced an 80% increase, and GST activity surged by 473%. Under aCO_2, with 120 mg/kg TI contamination, MTC levels rose, displaying a 123% increase ($P < 0.05$). Phytochelatins showed an increase of 88%, while GST activity increased by 304% compared to control levels ($P < 0.05$). For maize, MTC and phytochelatin levels, as well as GST activity, also saw significant increases under TI contamination. These parameters reached the highest values at 120 mg/kg TI treatment, which were 2.5, 2.3, and 5.1 times higher than eCO_2 alone, and 3.3, 2.6, and 3.5 times greater than aCO_2 alone ($P < 0.05$).

DISCUSSION

Effects of eCO_2 on TI accumulation. The investigation of the effects of eCO_2 and aCO_2 on TI contamination in wheat and maize reveals vital insights into the adaptive mechanisms employed by these crops to manage oxidative stress. This is particularly pertinent as heavy metals' exposure becomes increasingly common in agricultural settings. This study indicated that wheat and maize exhibited comparable

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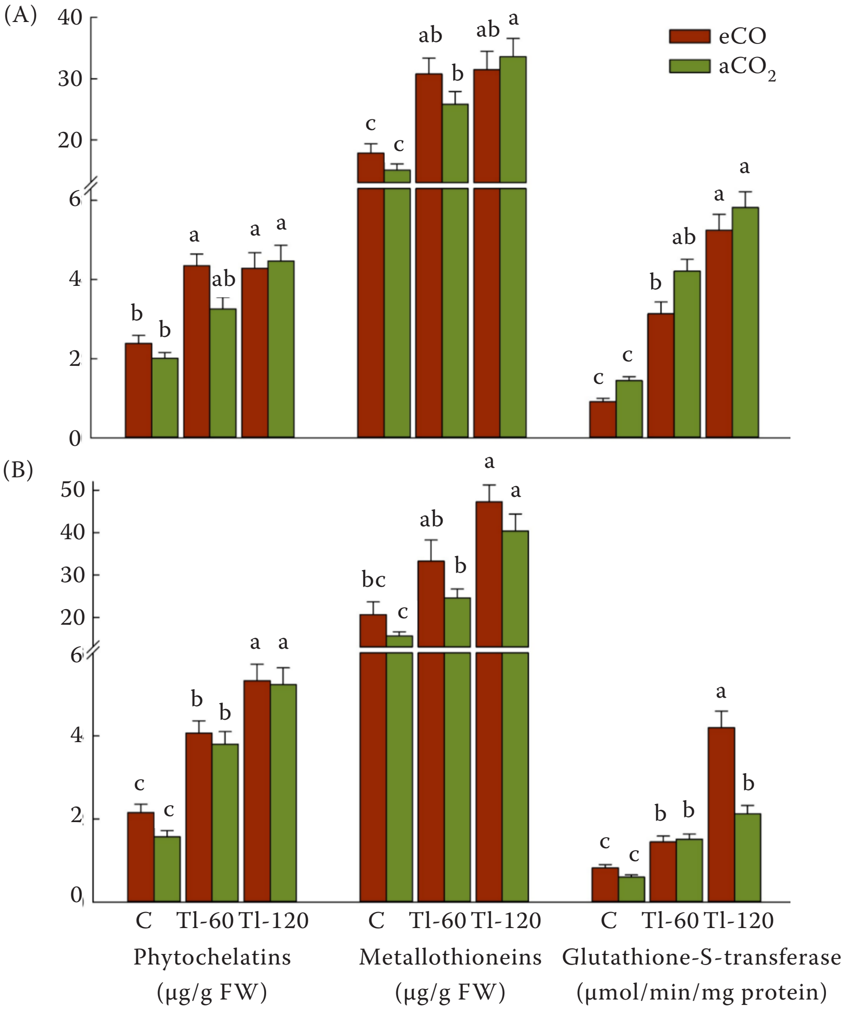

Figure 7. The effect of elevated CO_2 (eCO_2) and ambient CO_2 (aCO_2) conditions on detoxification activity in (A) wheat and (B) maize under different levels of soil thallium (TI) contamination. The means in each parameter with similar small letter(s) are not significantly different at 5% probability level (Tukey's *HSD* (honestly significant difference) test). C – control; Tl-60 – 60 mg Tl/kg; Tl-120 – 120 mg Tl/kg; FW – fresh weight

adaptations to eCO_2 relative to aCO_2, underscoring their similar physiological and biochemical strategies. Although TI naturally occurs in very low concentrations (Fergusson and Prucha 1990), elevated levels in soil negatively affect plant growth by inducing TI uptake and accumulation (Antisari et al. 2016). This accumulation impairs biomass production in crops like soybean, *Quercus pubescens*, *Brassica oleracea*, and mustard (Al-Najar et al. 2005, Vaněk et al. 2010). Although TI contamination negatively impacted the growth of both species, wheat demonstrated a more significant reduction in biomass, particularly at 120 mg/kg TI. These variations under metal stress support previous research that suggests responses to elevated CO_2 in the context of heavy metal toxicity can differ among plant species and specific varieties (Jia et al. 2010, Li et al. 2010, Albqmi et al. 2024). Contrary to speculative claims about enhanced Ti uptake and storage as an adaptive strategy, the increased Ti content in both crops under eCO_2 appears to reflect passive accumulation due to altered root physiology, such as reduced rhizosphere pH under eCO_2, which increases metal solubility (Yang et al. 2024). This is supported by soil post-treatment analysis, where Ti in the soil solution rose to 0.22 mg/L under eCO_2 from 0.15 mg/L in aCO_2 plots, indicating enhanced mobilisation. These findings align with Jia et al. (2010) and Li et al. (2010), who reported that eCO_2 can amplify heavy metal uptake by altering soil chemistry and root exudation. However, responses vary by species and variety (Yang et al. 2024). The differential responses of wheat and maize under TI stress and eCO_2 highlight the need for species-specific management strategies in contaminated agricultural systems. While eCO_2 may enhance photosynthetic efficiency and stress tolerance at low Ti levels, high Ti concentrations exacerbate nutrient deficiencies and oxidative stress, particularly in wheat. The increased photosynthetic activity under eCO_2 could lead to greater root growth and water uptake, which in turn might enhance the mass flow of Tl from the soil into the plant. To strengthen this mechanistic claim, the study's data should ideally include a direct correlation between these higher Tl levels and concurrent reductions in essential mineral content (e.g., potassium, magnesium) within the plant tissues.

High CO_2 improved photosynthesis and reduced photorespiration in TI-treated plants. We measured key physiological parameters to understand the reduction in plant biomass under contamination. Among them, the photosynthesis rate in both plants was significantly affected by TI contamination. However, eCO_2 showed a non-significant improvement compared to the same TI levels under aCO_2. A similar trend was observed in g_s, with notable increases in maize plants grown under eCO_2 compared to aCO_2 at 120 mg/kg TI. These minor differences in the response of the two plants to eCO_2 can be linked to their distinct photosynthetic mechanisms, as C3 and C4 plants possess varying physiological and biochemical traits that influence their interactions with CO_2 levels and responses to metal stress (Aloufi and Halawani 2025). Previous research has highlighted that C4 plants, like maize, gain advantages from efficient CO_2 fixation and reduced photorespiration levels, which enhance their resilience to abiotic stressors (Behera et al. 2022).

Moreover, both wheat and maize showed reductions in photosynthetic pigments with increasing levels of TI contamination, further corroborating the earlier observed biomass reductions. TI can disrupt chlorophyll integrity, cause necrosis symptoms, and interfere with nutrient uptake (Everaarts and Van Beusichem 1998, Rossel 2008, Abdel-Mawgoud et al. 2023). Elevated CO_2 conditions provided higher pigment concentrations under 120 mg/kg TI, highlighting the critical interplay between CO_2 levels and soil contamination on plant physiology. Previous studies have reported a reduction in photosynthetic pigment content and overall photosynthetic efficiency due to stress from environmental pollution, attributing these effects to disruptions in the photosynthetic electron transport chain and the generation of reactive oxygen species (ROS) in chloroplasts, which in turn affects the synthesis of photosynthetic pigments (Li et al. 2020, Albqmi et al. 2023). However, the enhancement of both enzymatic and non-enzymatic antioxidants, along with increased detoxification activity under TI contamination, has been linked to improved photosynthetic parameters in plants (Zhang et al. 2019, Madany et al. 2022). This suggests that the greater tolerance of plants grown in eCO_2 conditions to TI contamination may have contributed to a more effective photosynthesis of photosynthetic pigments than those grown under aCO_2 conditions.

The decline in the F_v/F_m ratio in TI-stressed plants negatively impacted PSII function. This ratio reflects the maximum efficiency of PSII in dark-adapted leaves, typically ranging from 0.79 to 0.85 in unstressed conditions (Yaghoubi et al. 2019); in this study, it was observed between 0.78 and 0.79 in unstressed plants. Notably, the stable F_v/F_m ratio in plants grown under eCO_2 with 60 mg/kg TI compared to control eCO_2 plants suggests that eCO_2 may help in regulating the distribution of excitation energy to the reaction centres in PSII, thereby mitigating photo-damage in leaves during stress (Yaghoubi et al. 2020).

To support these findings, the photorespiration pathway was examined as a significant source of ROS in the peroxisomes of stressed plants (Bapatla et al. 2021), focusing on the activities of GO and HPR, along with the Gly/Ser ratio under TI contamination. It was found that soil contamination with TI, especially at elevated levels, intensifies photorespiratory metabolism, particularly in conditions of aCO_2. This increase in key enzyme activity associated with photorespiration aligns with earlier studies on environmental pollution (D'Alessandro et al. 2013), indicating that photorespiration may help protect photosynthetic components from oxidative stress-induced over-reduction by facilitating excess energy dissipation in PSII (Hu et al. 2020, Bapatla et al. 2021). Furthermore, the elevated Gly/Ser ratio observed in TI-treated plants suggests that one of the plant's stress response mechanisms is actively managing nitrogen metabolism within leaves, which aids in the conversion of nitrogen into amino acids (Hu et al. 2020). This process is crucial for effectively allocating excitation energy under oxidative stress conditions (Hu et al. 2014).

High CO_2 maintained high redox status and etoxification mechanisms under Tl contamination. The results indicated that increased soil TI levels significantly enhanced oxidative markers, such as H_2O_2 and MDA, with aCO_2 conditions resulting in notably higher stress responses compared to eCO_2. This finding aligns with Abdel-Mawgoud et al. (2023), who indicated that TI exposure reduced growth and photosynthetic performance while increasing oxidative markers such as MDA and lipoxygenase (LOX) activity. The treatment with eCO_2 significantly reduced levels of oxidative markers in both plant species, especially at 20 mg/kg TI, highlighting its role in mitigating oxidative damage. This protective

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effect is likely due to improved detoxification of ROS in plants exposed to eCO_2 at higher TI levels, as antioxidant enzymes and compounds are more actively involved compared to those in untreated control plants. Nevertheless, elevated levels of H_2O_2 and MDA in both wheat and maize, particularly under aCO_2, point to the necessity of effective antioxidant defenses against stress. These results align with previous studies that have reported oxidative stress in crops due to heavy metal contamination, primarily because the resulting oxidative stress can surpass the capacity of the antioxidant enzyme system (He et al. 2022, Thiruvengadam et al. 2024). Additionally, the findings of this research echo those of earlier work that demonstrated the beneficial effects of eCO_2 in reducing oxidative marker concentrations in plants exposed to pollutants, such as heavy metals (Jia et al. 2010, Shabbaj et al. 2022).

The plant has to maintain high redox control to help plant growth and develop under biotic stress (Zinta et al. 2016). This outcome may be attributed to an increased detoxification of ROS in plants treated with eCO_2 under TI-induced oxidative stress, where certain antioxidant enzymes and metabolites, such as GSH, POX, APX, DHAR, and MDHAR in maize at 120 mg/kg TI, and POX, APX, MDHAR, and GR in wheat at 60 mg/kg TI, were more active compared to plants at the same TI levels grown under aCO_2. The connection between the detoxification of excess ROS and the enhancement of antioxidant defence mechanisms has been previously documented (Shabbaj et al. 2022). These findings suggest that eCO_2 boosts enzymatic antioxidant defences, particularly benefiting C4 plants under higher levels of TI contamination and C3 plants at lower levels.

Further examination of the antioxidant capacity of wheat and maize reveals that TAC, along with concentrations of polyphenols, flavonoids, and various enzymatic antioxidants, dramatically increased in response to TI contamination. Specifically, at 120 mg/kg TI, significant increments in TAC illustrate the enhanced ability of these crops to mitigate oxidative stress through increased synthesis of protective metabolites (AbdElgawad et al. 2023). It has been noted that plants with elevated levels of direct ROS-detoxifying enzymes (such as POX, SOD, and CAT) and those involved in the ASC/GSH pathway (including ASC, GSH, APX, DHAR, MDHAR, GR, and GPX) can endure the adverse effects of contamination over extended periods (Madnay et al. 2022). Nonetheless, the limited improvement observed in some components of antioxidant systems in response to soil TI contamination may be attributed to the sensitivity of these systems, particularly the ASC-GSH cycle. While they play a protective role against oxidative damage, they can be vulnerable under extreme stress conditions (El-Badri et al. 2022, Albqmi et al. 2023). Despite this, high concentrations of many of these molecules observed in the current study, particularly in TI-treated plants, appear to serve as a primary protective mechanism against contamination.

The mechanisms for detoxification involving PCs, MTC accumulation, and GST activity showed marked upregulation in response to TI contamination. In both plant types, the application of eCO_2 did not lead to significant changes in these detoxification measures compared to aCO_2 at the same TI concentrations, except for GST activity in eCO_2-treated maize, which was significantly greater than in those treated with aCO_2 at 120 mg/kg TI. Chia (2021) presented similar evidence highlighting significant metabolic alterations in crops exposed to heavy metal stress, thereby supporting that wheat and maize possess robust biochemical pathways to counteract TI-induced toxicity. Importantly, these findings underscore that the physiological responses to TI contamination clearly enhanced the detoxification activity across both CO_2 environments. The increase in PCs and MTC levels in TI-stressed plants supports previous research indicating the activation of a complex detoxification system in response to environmental pollutants. This system involves the chelation of metal ions by PCs and MTC within the cytosol, followed by their sequestration in the vacuole (Zhao and Chengcai 2011, Hasan et al. 2017). These protective molecules are structurally and functionally similar to GSH and are believed to be produced through the same biosynthetic pathway, with GSH serving as a substrate for their creation (Rauser 1999). Therefore, the elevated GSH levels in contaminated treated plants, particularly maize, may account for the increased PCs and MTC levels observed. Additionally, prior studies have indicated that PCs are vital for enhancing the efficiency of the GSH detoxification pathway in metal-contaminated plants (Madany et al. 2022). Moreover, the heightened activity of the GST enzyme in TI-stressed plants is consistent with findings from other studies that suggest the key role of GST in defending against oxidative damage by neutralising free radicals with the assistance of GSH during contamination-induced stress (Kumar and Trivedi 2018, Madany et al. 2022). These results underscore the regulatory function of these detoxifying metabolites in maintaining ROS balance within stressed plants.

Differential adaptive responses of C3 and C4 plants to TI toxicity. To further elucidate the differences in adaptive responses to Tl toxicity under eCO_2 conditions, it is crucial to highlight the distinct metabolic mechanisms employed by C3 and C4 plants. Wheat and maize showed fundamentally different photosynthetic pathways, significantly influencing their respective adaptive strategies to Tl toxicity under eCO_2. The C3 photosynthetic pathway is characterised by a greater susceptibility to photorespiration, particularly under stress conditions, which can exacerbate oxidative damage through increased production of ROS. In contrast, C4 plants like maize possess an efficient carbon fixation mechanism, which minimises photorespiration and enhances their ability to maintain higher photosynthetic efficiency even under elevated levels of Tl contamination. This efficiency translates to more effective oxidative stress management due to lower ROS accumulation. Moreover, the distinct biochemical pathways utilised by these two groups influence their metabolic responses; for instance, maize can allocate resources more effectively towards antioxidant production and detoxification pathways under stress. This suggests that the resilience mechanisms employed by C4 plants may afford them a significant advantage in adapting to the dual pressures of Tl toxicity and increased atmospheric CO_2. Understanding these differences facilitates better management strategies and emphasises the importance of selecting appropriate crop species or cultivars for sustainable agriculture under changing environmental conditions.

Study limitations. A limitation of the present study is the lack of consideration for the diluting effect of increased biomass and water volume on the concentration of TI contaminants within plant tissues. Specifically, metrics such as biomass-specific pollutant concentration were not employed, which could have offered a more comprehensive understanding of how TI is retained relative to biomass accumulation. The conventional approach of measuring total contamination may obscure the acute effects of TI toxicity, as higher biomass often results in greater dilution of the pollutant, thereby reducing its concentration within the plant. Despite this dilution, even low concentrations of TI can significantly disrupt metabolic functions and impair oxidative stress responses.

This limitation carries significant ecological and food safety implications, especially for Tl accumulation in edible grains and its transfer through the food chain. Our lack of biomass-specific concentrations might underestimate consumer and ecosystem risk. Increased biomass under eCO_2 could dilute Tl concentration per edible unit, but enhanced Tl uptake without proportional biomass increase could lead to dangerously high crop levels. A deeper research on Tl's direct impact on edible grains, its transfer to livestock, and ultimately to human consumers, is warranted for food safety assessments. Future research must rigorously quantify Tl in harvestable plant parts, considering biomass changes, to accurately assess dietary exposure risk and guide agricultural practices to ensure food security while minimising the health risks associated with heavy metal contamination under changing atmospheric CO_2 levels.

Conclusion and future perspectives. This investigation into the effects of eCO_2 and ambient CO_2 on Tl contamination in wheat and maize offers significant insights into the adaptive mechanisms crops employ to mitigate oxidative stress. Both species demonstrated comparable physiological and biochemical responses to eCO_2, contributing to their resilience against Tl-induced damage. Notably, while Tl contamination adversely affected growth, with wheat displaying a more pronounced reduction in biomass, the presence of eCO_2 generally supported the crops' capacity to counteract Tl's negative effects. The upregulation of antioxidant enzymes and metabolites under eCO_2 indicates a robust defence strategy, showcasing how enhanced CO_2 conditions can improve the capacity of these crops to manage oxidative stress and heavy metal toxicity to some extent. However, this mitigation did not lead to complete yield recovery, indicating that the protective role of eCO_2 has limits under the experimental conditions. This study provides valuable insights but acknowledges limitations regarding experimental scope and Tl exposure duration. This research focused on short-term responses in a controlled setting. Future studies should investigate long-term adaptive strategies and real-world complexities by incorporating field studies and multi-omics approaches. Understanding interactions among various stressors will enhance insights into plant resilience and aid in developing better agricultural practices. Additionally, future research must include biomass-specific metrics to clarify the interplay between biomass accumulation, pollutant concentration, and physiological resilience in Tl-contaminated crops.

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