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Species-specific responses of wheat and maize to thallium stress under elevated CO_2: effects on yield, photosynthesis, and metabolism

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Abstract: Heavy metal stress inhibits plant growth, but this impact is less studied and pronounced under climate change conditions. The present study investigates the physiological, biochemical, and agronomic responses of wheat (C3) and maize (C4) exposed to varying thallium (Tl) stress (60 and 120 mg/kg) under ambient (aCO_2) and elevated (eCO_2, 710 µmol/mol) CO_2 levels. High Tl exposure markedly reduced grain yield by 58% in wheat and 68% in maize at 120 mg/kg under aCO_2. However, eCO_2 partially offset the negative effects, increasing yield by ~20% in wheat and 36% in maize at 60 mg/kg Tl. eCO_2 enhanced photosynthetic activity under eCO_2, which increased the accumulation of soluble sugars under TI stress. These provide carbon skeletons for the synthesis of primary metabolites such as amino acids, organic acids and fatty acids. Although total fatty acid content declined under stress, the metabolic crosstalk initiated by improved photosynthesis and sugar availability enables plants to maintain key fatty acids (such as palmitic, linolenic, and oleic acids) essential for membrane stability and function. Amino acids, especially proline and cysteine, accumulated significantly under Tl stress. These primary metabolites, in turn, feed into secondary metabolic pathways, promoting the formation of phenolic acids and flavonoids that enhance antioxidant defence and stress tolerance. This metabolic cascade explains eCO_2's capacity to alleviate TI stress and improve crop performance, and underscores the value of leveraging eCO_2 environments to support agricultural productivity and food security under challenging conditions.

Keywords: C3 and C4 plants; environmental toxicity; physiological responses; *Triticum aestivum* L.; *Zea mays* L.

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Wheat (*Triticum aestivum* L.) and maize (*Zea mays* L.) are vital cereal crops known for their significant economic contributions and nutritional advantages (Grote et al. 2021, Jamali et al. 2021). These grains are abundant in essential nutrients, including carbohydrates, proteins, vitamins, essential amino acids, and unsaturated fatty acids (Sahu et al. 2023). Beyond these macronutrients, maize and wheat are also sources of bioactive phytochemicals, especially phenolic compounds, which offer numerous health benefits and enhance their nutraceutical profiles (Patra et al. 2023). However, the cultivation, yield, and long-term sustainability of these crops face critical challenges, particularly from toxic heavy metals (Mereu et al. 2021, Albqmi et al. 2023a, Wang et al. 2025a). The rising demand for metals in high-tech sectors has heightened concerns regarding soil pollution. Thallium (Tl), one of the toxic heavy metals, typically exists in minute concentrations (Abdel-Mawgoud et al. 2023). The toxicity of Tl can be linked to the chemical resemblance of TI to potassium (K). Due to the nearly identical ionic radii of Tl and K, plants may inadvertently take up Tl instead of K, resulting in its accumulation within plant tissues. This situation is worsened by Tl's prevalent use in various industrial applications.

Simultaneously, atmospheric carbon dioxide (CO_2) levels are escalating due to industrial growth, fossil fuel dependence, and suboptimal agricultural practices. CO_2 concentrations have surged from approximately 280 μmol/mol CO_2 to about 416 μmol/mol CO_2, with predictions indicating potential levels over 700 μmol/mol CO_2 by the century's end (Shabbaj et al. 2022). This rise in CO_2 is a principal driver of climate change, provoking increasingly severe climatic events such as floods, drought, and heatwaves (Hagagy and AbdElgawad 2024). Elevated CO_2 conditions are now recognised as crucial factors in crop production, altering growth dynamics, biomass accumulation, photosynthesis, and metabolite profiles in plants, even under non-stressed conditions (Kaur et al. 2023, Hagagy and AbdElgawad 2024).

The present study examines the differences between C3 and C4 plants, focusing on their distinct photosynthetic responses to environmental stresses, such as Tl toxicity and elevated CO_2 (eCO_2). Furthermore, C3 and C4 plants possess distinct mechanisms for photosynthesis, which influence their adaptation to increased CO_2 levels. For instance, C4 plants tend to have efficient photosynthesis in eCO_2 conditions, often leading to higher biomass production when compared to C3 species in similar settings (Gowik and Westhoff 2011). Several studies indicate that wheat also benefits from eCO_2, showing enhancements in photosynthetic efficiency, lower transpiration rates, and improved overall productivity, which contributes to increased grain yields (Alsherif et al. 2023). Prior research indicates that cereal crops demonstrate increased grain yield and kernel weight at eCO_2 levels in favourable conditions, with evidence suggesting an increased number of grains compared to the mass of grains (Broberg et al. 2019, Blandino et al. 2020). Furthermore, investigations have identified physiological mechanisms linked to cereal crops enhanced yield under elevated CO_2, particularly regarding bioactive compounds and antioxidants biosynthesis (Wang et al. 2013, Dubey et al. 2015) in non-stressed environments (Blandino et al. 2020). Sreeharsha et al. (2019) noted that increased carbon availability under eCO_2 improves plant growth by boosting sink capacity and the ability to assimilate nitrogen. Improvements in photosynthetic efficiency and efficiency of photosystem II have been observed under elevated CO_2, supported by enhanced chlorophyll fluorescence metrics (Sekhar et al. 2015).

This study aims to investigate the interactions between TI toxicity and elevated CO_2 levels to improve cereal crop management strategies that address environmental challenges and promote sustainable agriculture amidst climate change. Specifically, it will explore the physiological, biochemical, and agronomic responses of maize and wheat when exposed to varying concentrations of TI in conjunction with elevated CO_2. The research will assess how TI influences growth, photosynthesis parameters and metabolic profiles, and evaluate the potential mitigating effects of elevated CO_2 on TI-induced stress. We hypothesise that increased CO_2 will alleviate some negative physiological impacts of TI exposure by enhancing photosynthetic functionality and boosting biochemical properties, ultimately leading to improved growth and yield.

MATERIAL AND METHODS

Plant materials and experimental setup. Wheat (*Triticum aestivum* L. var. Giza 119) and maize (*Zea mays* L. var. Giza 2) seeds were sourced from the Centre of Agricultural Research (Giza, Egypt). For the study, a completely randomised design with three replicates was utilised, examining two main factors: soil TI contamination (0, 60, and 120 mg/kg) and variable atmospheric CO_2 concentrations (control at 410 µmol/mol CO_2 and elevated levels at 710 µmol/mol CO_2). The TI levels were chosen based on our previous study (Obaid et al. 2025). The experimental soil was classified as a clay/silt loam, consisting of approximately 54% clay, 36% silt, and 10% sand based on particle-size analysis performed using the hydrometer method. The soil texture indicates a fine-textured soil with substantial clay and silt fractions, characteristic of good water retention and nutrient-holding capacity. The original soil used had the following physicochemical properties: electrical conductivity (EC) of 2.01 dS/m, pH 6.98, calcium carbonate ($CaCO_3$) content of 12.1 g/kg, organic carbon content of 1.03 g/kg, total nitrogen 126.7 mg/kg, ammonium nitrogen (NH_4-N) 7.1 mg/kg, sodium 0.207 g/kg, total phosphorus 71.2 mg/kg, potassium 62.1 mg/kg, calcium 10 mg/kg, magnesium 4.1 g/kg, and iron 1.1 mg/kg. The soil's cation exchange capacity (CEC), an important parameter for nutrient retention and soil fertility, was measured at 23 $mmol_+$/100 g. For pot experiments, 500 g of this well-characterised soil was used to fill each container, which was then spiked with TI nitrate ($TlNO_3$). Additionally, CO_2 was infused into the chamber's airflow to maintain the desired CO_2 levels throughout the experiment. In each pot, five wheat plants (35 cm in diameter) and two maize plants (50 cm in diameter) were arranged, with specific temperature and light parameters established to promote optimal growth conditions. Wheat was cultivated at temperatures ranging from 20–25 °C with 16 h of light daily, while maize was grown at 25–30 °C with the same light duration. After a growing period, wheat and maize plants were harvested at 120 and 130 DAS (days after sowing), respectively.

Agronomic and photosynthetic parameters. During the harvest period, plants were taken from each pot to assess grain yield per plant, as well as grain weight and the number of grains per plant. Photosynthetic parameters were measured in wheat flag leaves and maize plants' ear leaves at 75 and 85 DAS during the grain-filling phase (post-anthesis), respectively. The levels of chlorophyll and carotenoids were analysed through a spectrophotometric method adapted from the Porra technique (Porra 2002), using a Synergy Mx microplate reader (Yaghoubi et al. 2019). Additionally, photosynthetic rate (P_n) was determined (LI-COR 6400/XT, Lincoln, USA). A settling period of 30 min was allowed before taking measurements to facilitate acclimatisation. Light levels were 800 µmol photons/m^2/s for wheat and 1 000 µmol photons/m^2/s for maize, considering their different requirements for photosynthetic saturation. Throughout the measurement, leaf temperature was kept at a steady 25 °C to ensure reliable physiological responses. CO_2 concentrations were maintained at 410 and 710 µmol/mol for the control group and eCO_2-treated plants, respectively, facilitating a precise assessment of the experimental goals.

Determination of mineral accumulation in grains. The nutrient concentrations in plants were measured employing spectrometry (total-reflection X-ray fluorescence, Berlin, Germany), ion chromatograph (Shimadzu, Kyoto, Japan), and the Kjeldahl method, as described by Yoshida et al. (2016) and Bamrah et al. (2019).

Grain protein quantification. To extract total protein from dehydrated wheat and maize grains, mature grains were ground and pulverised in liquid nitrogen. Sequential extraction utilised three buffers: buffer A1 for albumins, buffer A2 for globulins, and buffer B for prolamins/glutelins, with each fraction obtained after centrifugation (14 000 *g* for 23 min, 5 °C). Albumin and globulin fractions were quantified using a Coomassie Plus (Bradford) Assay, measuring absorbance at 595 nm. Prolamin/glutelin fractions, requiring dilution due to SDS presence, were quantified *via* the DC Protein Assay, measuring absorbance at 750 nm (Santos et al. 2017).

Assessment of carbohydrate content. Soluble sugars were extracted using 80% ethanol (*v*/*v*) at a temperature of 80 °C for 60 min. After extraction, anthrone reagent (anthrone (100 mg) in H_2SO_4 (50 mL concentrated H_2SO_4) was added. The remaining pellet, obtained after the soluble sugar extraction, was utilised to assess starch content (Galtier et al. 1995). The starch solution was hydrated and gelatinised with 92% dimethyl sulfoxide, followed by precipitation and washing with ethanol. After centrifugation and vacuum drying at 28 °C, the starch was treated with a blend of α-amylase and amyloglucosidase to extract it. Using spectrophotometric methods, total soluble sugars and starch were quantified using a multi-mode microplate reader (Synergy Mx, Biotek, Santa Clara, USA). The activity of α-amylase was measured using the Ceralpha method (McCleary and Sheehan 1987).

Assessment of primary metabolites in grains. The fatty acids were extracted and measured in grain samples (Torras-Claveria et al. 2014). In this process, samples extracted in methanol contain nonadecanoic acid as an internal standard. The analysis was executed using gas GC-MS of a Hewlett-Packard 6890 system

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linked with an MSD 5975 mass spectrometer. Fatty acids were identified by comparing them to the NIST 05 and Golm Metabolome databases.

The method described by Zinta et al. (2018) was followed to evaluate the amino acid profile. In brief, ground grain samples were mixed with 80% (*v*/*v*) ethanol. The extracted samples were centrifuged (4 000 rpm for 18 min). The pellet obtained was resuspended in chloroform after the supernatant had undergone vacuum evaporation. The supernatant, collected after a subsequent centrifugation (3 800 rpm for 11 min), was filtered through a Millipore microfilter with a 0.2 μm pore size and diluted with deuterated L-glutamine-2,3,3,4,4-d5, which acted as the internal standard. The detection, separation, and quantification of amino acids were measured by the Waters Acquity UPLC-TQD system (Milford, USA) with a BEH amide column (Zinta et al. 2018).

The quantification of organic acids in the grain samples was conducted after extraction with a 0.1% (*v*/*v*) phosphoric acid solution 28 min, 4 °C), and the samples were filtered and analysed using isocratic HPLC with 0.0005 mol sulfuric acid, operating at a wavelength of 210 nm and a flow rate of 0.6 mL per minute (Sturm et al. 2003). For separation, an Aminex HPH-87 H column (310 mm × 7.7 mm) was used alongside a Bio-Rad IG Cation H pre-column (30 mm × 4.6 mm), maintained at a temperature of 65 °C.

Assessment of antioxidant metabolite level. According to AbdElgawad et al. (2020) and Zhang et al. (2006), flavonoid and polyphenol levels were measured using aluminium chloride colourimetric and Folin-Ciocalteu assays, respectively. In addition, tocopherol content in the plant extracts was analysed *via* HPLC (Shimadzu, Hertogenbosch, the Netherlands), following the guidelines by AbdElgawad et al. (2015). For this analysis, dimethyl tocol (DMT) was utilised as an internal standard at a concentration of 5 ppm.

Statistical analysis. Analyses were performed using SigmaPlot software (San Jose, USA). Two-way analysis of variance (ANOVA), implementing Tukey's honestly significant difference (*HSD*) test, and creating graphs were performed. Data (mean ± standard deviation) with a significance level (α) of 0.05 set for both the Tukey's test and correlation analyses.

RESULTS

Grain yield. The present study showed that the wheat grain yield was higher under eCO_2, especially under 60 mg/kg soil TI contamination (Figure 1). The highest yield was under eCO_2 (with approximately a 15% increase over aCO_2; $P \geq 0.05$), while the lowest yield was observed under 120 mg/kg Tl contamination in aCO_2-treated plants, representing a drop of about 50% and 42% from the eCO_2 and aCO_2 alone ($P < 0.05$). For maize, a similar trend was evident; eCO_2 conditions yielded a higher grain production compared to aCO_2, showing a difference of around 29% ($P < 0.05$), 36% ($P < 0.05$), and 21% ($P < 0.05$) compared to no contamination, 60 mg/kg TI and 120 mg/kg TI in aCO_2-treated plants, respectively. Similar trends were observed for grain weight, in which the grain weight in plants treated with 120 mg/kg TI was significantly lower compared to the control under both eCO_2 and aCO_2 conditions (Figure 1).

Photosynthetic parameters. Net photosynthetic rates in wheat were optimal in eCO_2, showing a decrease of about 47% when Tl contamination was increased to 120 mg/kg, compared to the highest eCO_2 values ($P < 0.05$) (Figure 2). A reduction under aCO_2 was about 47% ($P < 0.05$). In contrast, maize also showed a superior net photosynthetic rate under eCO_2, decreasing by about 34% under the highest Tl concentration compared to eCO_2 alone ($P < 0.05$) (Figure 2).

Although, the content of chlorophyl (Chl) *a* in eCO_2-treated wheat plants was not affected compared to aCO_2 in non-contamination conditions, its content was significantly lower under 120 mg/kg TI compared to control is response to both eCO_2 (–36%) and aCO_2 (–38%) conditions, highlighting the detrimental effect of Tl on Chl *a* pigment accumulation (Figure 2). In contrast, Chl *a* content in maize plants remained unchanged in response to TI contamination, while significantly higher (+ 29%) in eCO_2-treated plants than in aCO_2 under no contamination conditions. However, Chl *b* in both plants was significantly declined at higher levels of TI contamination (except for maize under aCO_2), and the carotenoid accumulation was high under 120 mg/kg TI contamination in both plants ($P < 0.05$) (Figure 2).

Mineral and metal content in grains. The analysis of mineral and metal content revealed that both plants demonstrated notably higher levels of some of the studied elements under eCO_2 conditions than aCO_2 in response to TI contamination (Table 1). Specifically, phosphorus levels showed a decrease of approximately 21% and 38% in wheat, and 12% ($P \geq 0.05$) and 44% in maize grains under 120 mg/kg Tl contamination compared to the eCO_2 and eCO_2

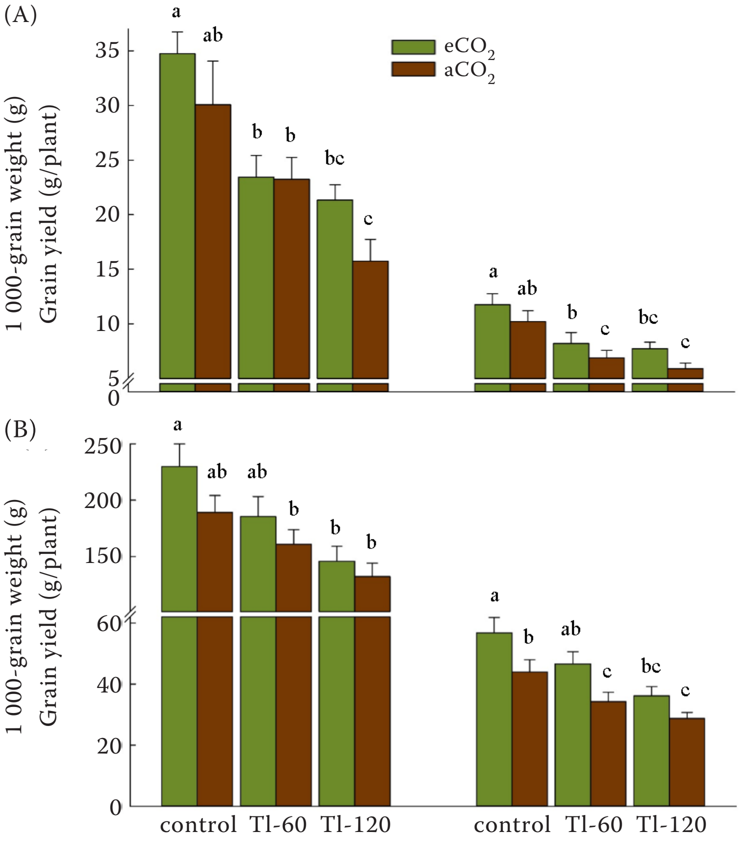

Figure 1. The effect of different CO_2 levels and soil thallium (Tl) contamination on grain yield and grain weight of (A) wheat and (B) maize plants. The means (± standard deviation) in each parameter with similar small letter(s) are not significantly different at 5% probability level (Tukey's test *HSD* test). eCO_2 – elevated CO_2; aCO_2 – ambient CO_2; control – no contamination; Tl-60 – 60 mg Tl/kg; Tl-120 – 120 mg Tl/kg

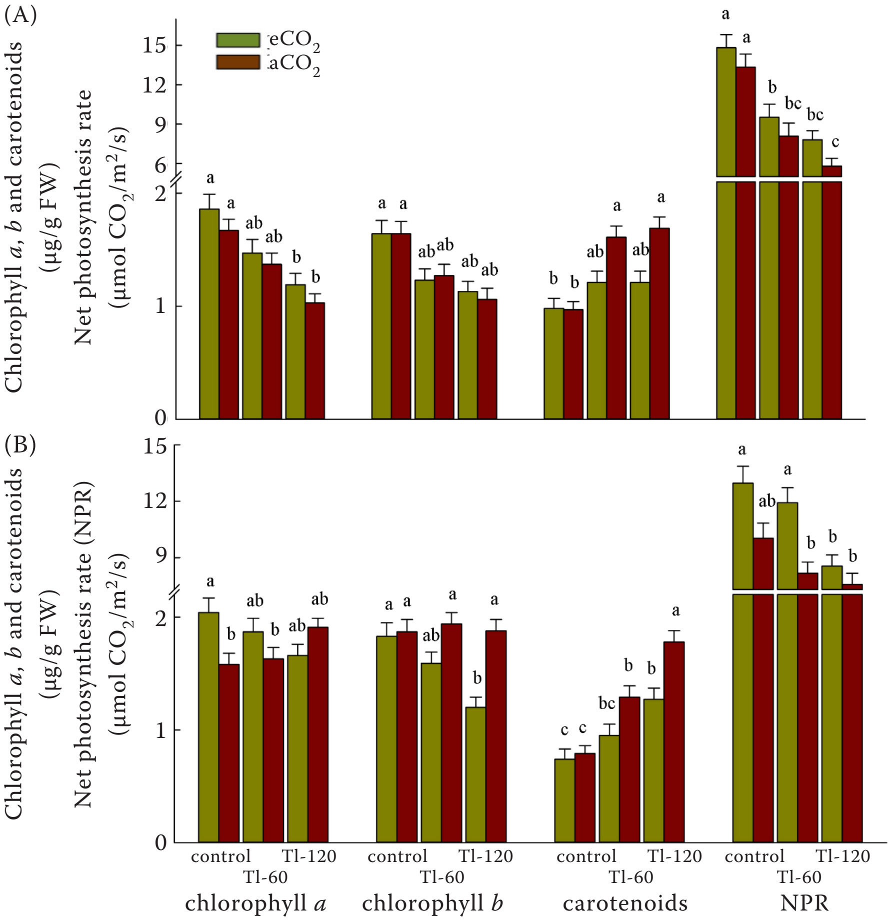

Figure 2. The effect of different CO_2 levels and soil thallium (Tl) contamination on photosynthetic parameters of (A) wheat and (B) maize plants. The means (± standard deviation) in each parameter with similar small letter(s) are not significantly different at 5% probability level (Tukey's test *HSD* test). eCO_2 – elevated CO_2; aCO_2 – ambient CO_2; control – no contamination; Tl-60 – 60 mg Tl/kg; Tl-120 – 120 mg Tl/kg; FW – fresh weight

Table 1. The effect of CO$_2$ levels and soil thallium (TI) contamination on nutrient and metal content (± standard deviation) in the grains of wheat and maize plants

Parameter	Elevated CO$_2$			Ambient CO$_2$		
	control	TI (60 mg)	TI (120 mg)	control	TI (60 mg)	TI (120 mg)
Wheat						
Phosphorus (g/kg)	5.49 ± 0.45^{a}	4.63 ± 0.43^{ab}	4.36 ± 0.35^{b}	5.59 ± 0.51^{a}	3.34 ± 0.29^{c}	3.46 ± 0.34^{c}
Sulfur (g/kg)	1.44 ± 0.15^{a}	1.20 ± 0.15^{ab}	1.02 ± 0.10^{b}	1.48 ± 0.17^{a}	1.05 ± 0.09^{b}	0.86 ± 0.12^{b}
Potassium (g/kg)	3.23 ± 0.24^{a}	2.87 ± 0.27^{ab}	2.32 ± 0.33^{b}	3.45 ± 0.31^{a}	2.40 ± 0.33^{b}	2.29 ± 0.25^{b}
Magnesium (g/kg)	4.80 ± 0.35^{a}	4.40 ± 0.41^{a}	3.90 ± 0.50^{ab}	4.50 ± 0.35^{a}	3.20 ± 0.33^{b}	2.81 ± 0.45^{b}
Calcium (g/kg)	0.85 ± 0.07^{bc}	1.06 ± 0.11^{ab}	1.24 ± 0.11^{a}	0.67 ± 0.09^{c}	1.01 ± 0.07^{b}	1.21 ± 0.12^{a}
Zinc (mg/kg)	8.02 ± 0.77^{a}	7.65 ± 0.65^{a}	7.80 ± 0.71^{a}	9.49 ± 1.13^{a}	8.68 ± 0.88^{a}	8.92 ± 0.93^{a}
Iron (mg/kg)	25.06 ± 2.32^{a}	28.13 ± 3.43^{a}	25.70 ± 3.11^{a}	25.69 ± 2.77^{a}	30.45 ± 3.01^{a}	30.58 ± 2.86^{a}
Copper (mg/kg)	7.18 ± 0.66^{a}	6.41 ± 0.71^{a}	5.77 ± 0.85^{ab}	6.69 ± 0.74^{a}	4.72 ± 0.56^{b}	4.18 ± 0.51^{b}
Manganese (mg/kg)	2.03 ± 0.21^{a}	2.45 ± 0.39^{a}	2.27 ± 0.22^{a}	1.92 ± 0.30^{a}	2.28 ± 0.25^{a}	2.21 ± 0.29^{a}
TI (mg/kg)	0.00 ± 0.00^{d}	16.13 ± 1.44^{c}	28.98 ± 2.33^{b}	0.00 ± 0.00^{d}	19.79 ± 2.22^{c}	58.14 ± 4.12^{a}
Maize						
Phosphorus (g/kg)	6.57 ± 0.44^{a}	5.69 ± 0.61^{a}	5.81 ± 0.71^{a}	6.08 ± 0.55^{a}	4.05 ± 0.34^{b}	3.40 ± 0.46^{b}
Sulfur (g/kg)	1.78 ± 0.14^{a}	1.51 ± 0.19^{ab}	1.51 ± 0.17^{ab}	1.54 ± 0.18^{ab}	1.43 ± 0.20^{ab}	1.25 ± 0.12^{b}
Potassium (g/kg)	3.53 ± 0.25^{a}	3.16 ± 0.31^{ab}	2.92 ± 0.36^{ab}	3.05 ± 0.38^{ab}	2.90 ± 0.31^{ab}	2.61 ± 0.20^{b}
Magnesium (g/kg)	2.76 ± 0.24^{a}	2.64 ± 0.28^{a}	2.60 ± 0.20^{a}	2.49 ± 0.31^{ab}	1.93 ± 0.26^{b}	1.90 ± 0.24^{b}
Calcium (g/kg)	2.66 ± 0.31^{b}	2.74 ± 0.27^{b}	3.87 ± 0.33^{a}	1.75 ± 0.19^{c}	3.38 ± 0.45^{ab}	3.76 ± 0.33^{a}
Zinc (mg/kg)	8.64 ± 0.90^{a}	8.84 ± 0.77^{a}	8.82 ± 0.81^{a}	7.87 ± 0.76^{a}	8.79 ± 0.65^{a}	8.17 ± 0.54^{a}
Iron (mg/kg)	39.99 ± 2.88^{a}	40.31 ± 3.92^{a}	41.11 ± 2.63^{a}	30.48 ± 3.11^{b}	30.30 ± 2.18^{b}	29.53 ± 1.88^{b}
Copper (mg/kg)	20.84 ± 2.89^{a}	15.77 ± 2.09^{ab}	15.14 ± 1.56^{b}	14.40 ± 1.99^{bc}	11.45 ± 1.77^{c}	11.28 ± 1.89^{c}
Manganese (mg/kg)	2.82 ± 0.24^{a}	3.29 ± 0.35^{a}	2.70 ± 0.36^{a}	2.84 ± 0.28^{a}	2.91 ± 0.33^{a}	3.31 ± 0.31^{a}
TI (mg/kg)	0.00 ± 0.00^{e}	13.62 ± 1.24^{d}	35.73 ± 2.89^{b}	0.00 ± 0.00^{e}	24.39 ± 2.76^{c}	51.10 ± 4.11^{a}

Means sharing the different letter(s) are significantly different ($P < 0.05$)

control, respectively ($P < 0.05$). Significant reductions were found of around 28% and 35% for potassium and 29% and 42% for sulfur in wheat grains under the same treatment ($P \geq 0.05$), while remaining unchanged in maize grains ($P \geq 0.05$). Furthermore, wheat displayed similar calcium levels across eCO$_2$ treatments when compared to the calcium content of both plants. At the same time, maize exhibited a more pronounced response, showing a substantial increase in calcium concentration to about 41% at 120 mg/kg Tl under eCO$_2$ conditions. This suggested that maize has a greater potential for calcium accumulation under TI contamination than wheat.

Moreover, wheat exhibited a significant increase in Tl content from control to the 120 mg/kg Tl treatment, with an increase of approximately 80% and 194% from the 60 mg/kg to the 120 mg/kg level under eCO$_2$ and aCO$_2$ conditions, respectively. In comparison, maize demonstrated an even greater sensitivity to Tl accumulation, with contamination increasing by about 162% and 109% from the 60 mg/kg to the 120 mg/kg treatment under eCO$_2$ and aCO$_2$ conditions, respectively ($P < 0.05$). This indicates that both plants reacted more positively under 120 mg/kg TI contamination at eCO$_2$ compared to aCO$_2$, with maize even showing a relative decrease in Tl content in response to the 60 mg/kg TI contamination level under eCO$_2$ ($P < 0.05$).

Sugar content and related enzyme activity. The total soluble sugar content in both plants was highest under 120 mg/kg Tl contamination in response to both eCO$_2$ and aCO$_2$ conditions, showing an increase of approximately 57% and 80% in wheat and 53% and 114% in maize grains compared to the eCO$_2$ and aCO$_2$ controls, respectively (Figure 3). These results also suggested that while high levels of Tl promote soluble sugar accumulation, eCO$_2$ did not affect this process ($P < 0.05$). Moreover, both plants exhibited non-significant reductions in starch content in grains from Tl-contaminated soil under

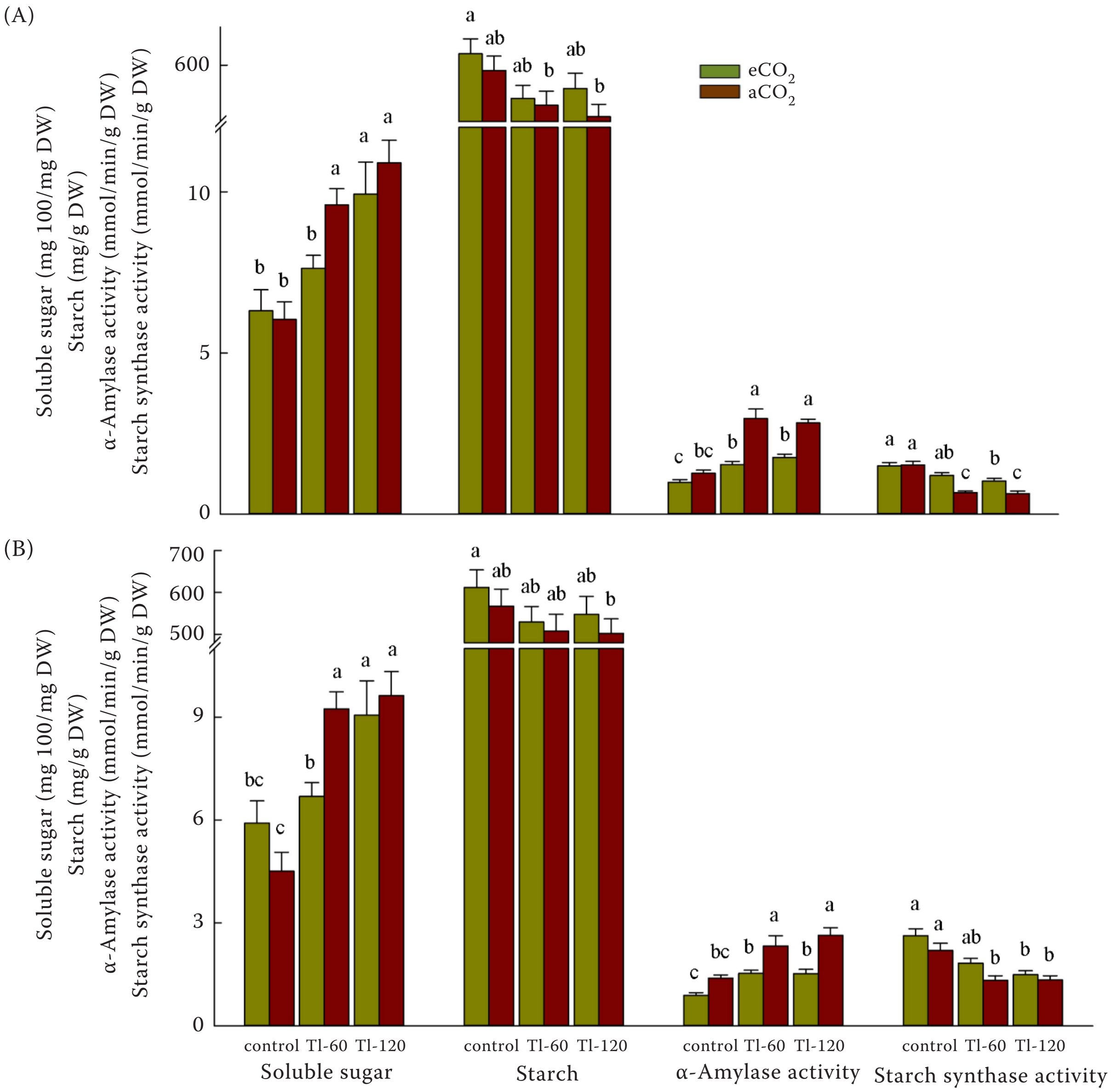

Figure 3. The effect of different CO$_2$ levels and soil thallium (TI) contamination on sugar metabolism of the grains of (A) wheat and (B) maize plants. The means (± standard deviation) in each parameter with similar small letter(s) are not significantly different at 5% probability level (Tukey's test *HSD* test). eCO$_2$ – elevated CO$_2$; aCO^2 – ambient CO$_2$; control – no contamination; Tl-60 – 60 mg Tl/kg; Tl-120 – 120 mg Tl/kg; DW – dry weight

eCO$_2$ and aCO$_2$ conditions ($P \geq 0.05$). However, there was a significant decrease in the activity of starch synthase, due to Tl contamination, particularly at 120 mg/kg Tl (–32–58%) ($P < 0.05$). In contrast, α-amylase enzyme activity significantly increased at both levels of TI contamination under both aCO$_2$ and eCO$_2$ conditions ($P < 0.05$) (Figure 3).

Profile of amino acid, fatty acid and storage proteins in grains. The hierarchical clustering analysis indicated notable shifts in the amino acid and fatty acid composition of wheat and maize grains due to varying CO$_2$ and TI contamination levels, with heat maps illustrating the differences among the treatments (Figures 4 and 5). In this regard, the impact of eCO$_2$ and Tl contamination on amino acid profiles in wheat and maize grains revealed significant variations in key amino acids essential for protein quality and plant metabolism. For instance, although the proline levels in grains remained unchanged in response to eCO$_2$, they increased by approximately 40–51% and 31–70% at 60 mg/kg Tl, and by 51–56% and 70–158% at 120 mg/kg Tl in wheat and maize grains, respectively, reflecting an enhanced ability to cope with TI stress ($P < 0.05$). Similarly, cysteine,

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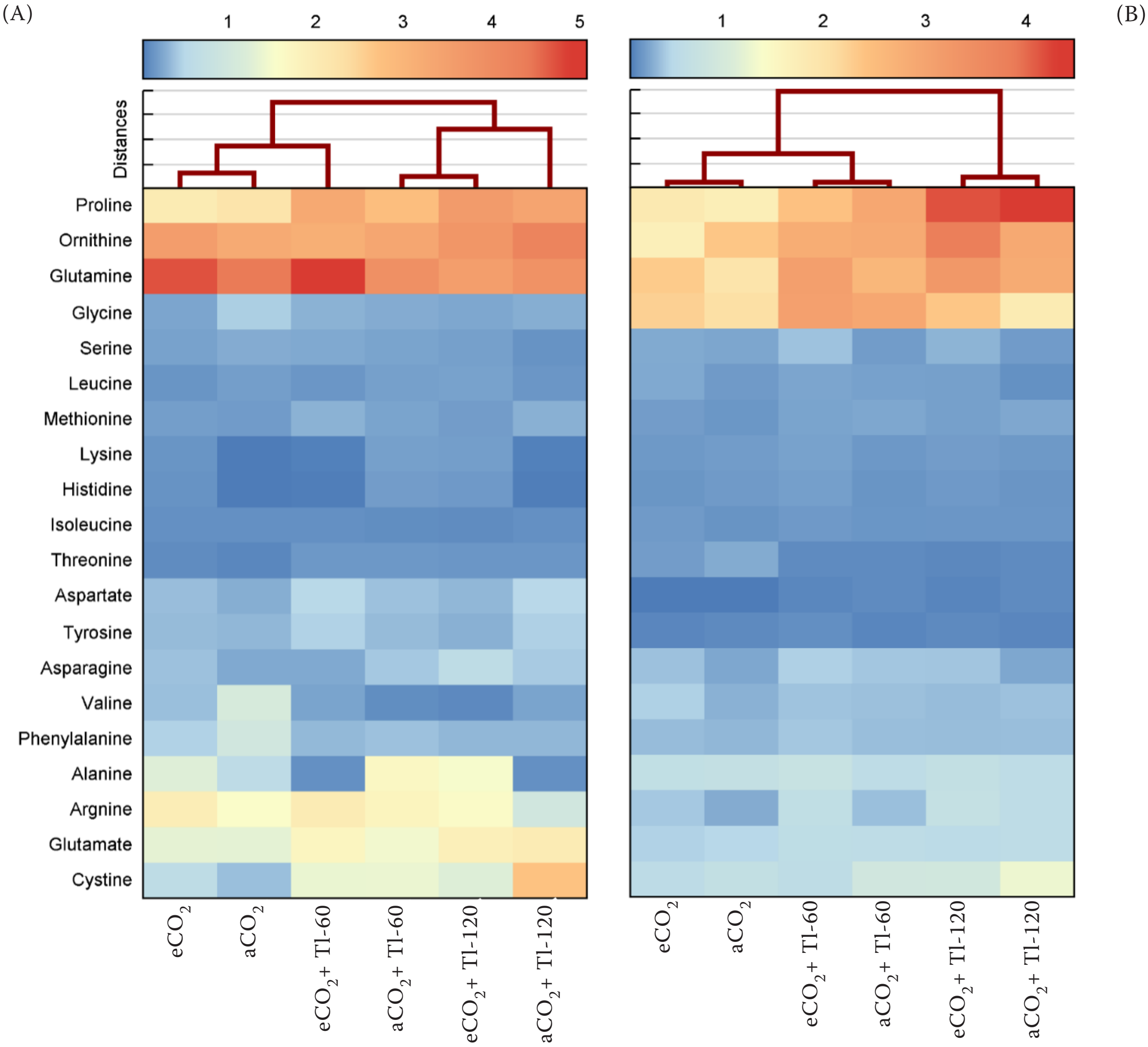

Figure 4. A hierarchical clustering analysis illustrates the variations in amino acid composition in the grains of (A) wheat and (B) maize plants in response to different CO_2 levels and soil thallium (TI) contamination. At the bottom of the panel, a colour gradient, ranging from 0 to 5, represents the amino acid content measured in mg per 100 mg of protein. eCO_2 – elevated CO_2; aCO_2 – ambient CO_2; Tl-60 – 60 mg Tl/kg; Tl-120 – 120 mg Tl/kg

crucial for protein synthesis and defence against oxidative stress, also increased under both eCO_2 and Tl contamination ($P < 0.05$). Likewise, other amino acids, such as glutamate and asparagine, vital for nitrogen metabolism, transport, and storage, were more accumulated in the grain under eCO_2 and TI contamination than in the same TI levels of those aCO_2-treated.

Apart from globulin in wheat grain, other storage proteins, including albumin, prolamin and glutelin in wheat and maize grains, were not affected by eCO_2 and soil contamination treatments. The highest value in globulin content was observed under no contamination in each CO_2 level, representing an approximate decrease of around 39–46% at 60 mg/kg TI and 50–54% at 120 mg/kg TI compared to those treated with eCO_2 and aCO_2 under no contamination ($P < 0.05$) (Table 2).

The three most abundant fatty acids identified in the grains in both plants were palmitic acid, linolenic acid, and oleic acid. Both wheat and maize exhibited significant declines in most saturated fatty acid levels under Tl exposure. Specifically, stearic acid content in the grains of both plants exhibited a notable decrease up to 32% at 120 mg/kg TI. In comparison, palmitic acid only reduced about 22% at 120 mg/kg

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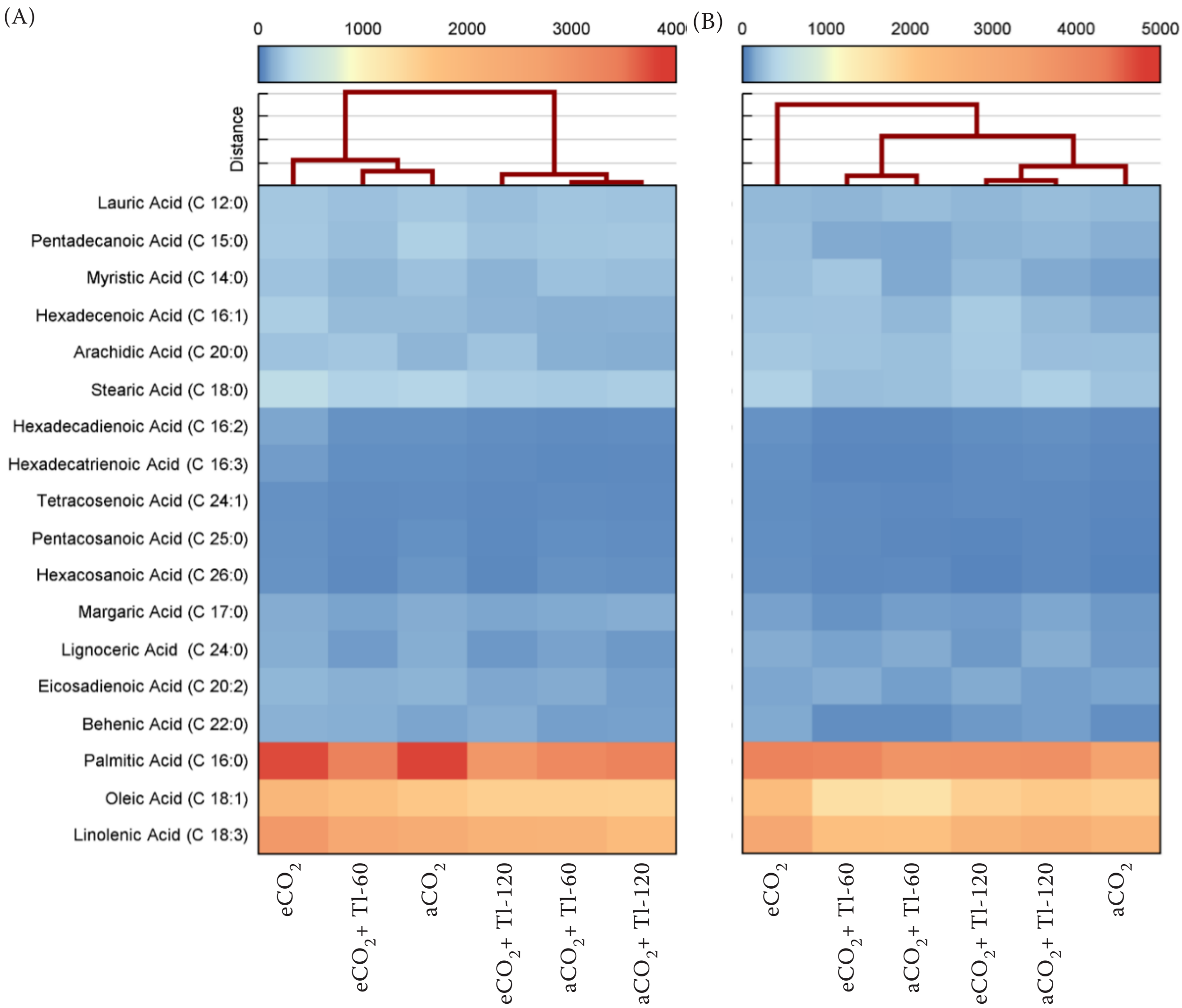

Figure 5. A hierarchical clustering analysis illustrates the variations in fatty acid composition in the grains of (A) wheat and (B) maize plants in response to different CO_2 levels and soil thallium (TI) contamination. At the bottom of the panel, a colour gradient, ranging from 0 to 5 000, represents the fatty acid content measured in μg/g FW (fresh weight). eCO_2 – elevated CO_2; aCO_2 – ambient CO_2; Tl-60 – 60 mg Tl/kg; Tl-120 – 120 mg Tl/kg

TI in wheat grains. In wheat grains, linolenic acid and oleic acid exhibited declines of about 39–47% and 17–24%, respectively, at 120 mg/kg TI under elevated CO_2 conditions. In contrast, the content of these unsaturated fatty acids remained unaffected in maize grains.

Antioxidant metabolites in grains. Some of the studied antioxidant metabolites were significantly influenced by Tl contamination in wheat and maize, while none were affected by eCO_2 treatment (Table 3). In this regard, polyphenol concentrations in wheat grains reached the highest values at 120 mg/kg TI, showing an increase of approximately 60% and 64% in eCO_2 and aCO_2 treated plants compared to the control at the same CO_2 levels ($P < 0.05$). Nevertheless, these treatments in maize grain did not show significant differences ($P \geq 0.05$). Both plants' flavonoid and β-tocopherol levels were relatively stable across CO_2 and TI treatments, with only a minor non-significant increment under TI contamination ($P \geq 0.05$). While alpha tocopherol concentration in grains was not affected by TI under eCO_2 ($P \geq 0.05$), their content significantly increased in TI and aCO_2 conditions, with increases up to 35% in wheat and 69% in maize grains ($P < 0.05$).

Organic acid contents in grains. Succinate and lactate levels in wheat grains showed non-significant changes in response to TI and eCO_2 ($P \geq 0.05$), while

Table 2. The effect of CO_2 levels and soil thallium (TI) contamination on storage proteins (mg/g Pr) in the grains of wheat and maize plants

Parameter	Elevated CO_2			Ambient CO_2		
	control	TI (60 mg)	TI (120 mg)	control	TI (60 mg)	TI (120 mg)
Wheat						
Albumin	51.44 ± 5.78^{a}	59.66 ± 6.11^{a}	68.06 ± 8.29^{a}	50.77 ± 6.36^{a}	55.84 ± 5.15^{a}	64.31 ± 5.83^{a}
Globulin	114.93 ± 10.23^{a}	70.45 ± 9.27^{bc}	57.62 ± 6.77^{cd}	91.13 ± 10.64^{ab}	49.31 ± 4.11^{d}	41.95 ± 4.04^{d}
Prolamin	255.40 ± 32.28^{a}	156.55 ± 18.29^{b}	128.05 ± 19.57^{bc}	202.51 ± 20.89^{a}	103.78 ± 11.47^{c}	83.79 ± 9.94^{c}
Glutelin	441.19 ± 45.76^{a}	297.89 ± 26.10^{b}	269.44 ± 32.19^{bc}	372.57 ± 40.18^{a}	238.77 ± 25.60^{c}	222.91 ± 28.91^{c}
Maize						
Albumin	34.35 ± 4.19^{ab}	34.57 ± 3.87^{ab}	44.05 ± 5.58^{a}	30.72 ± 3.72^{b}	34.11 ± 4.80^{ab}	39.83 ± 3.39^{ab}
Globulin	102.27 ± 10.37^{a}	84.90 ± 9.92^{ab}	75.25 ± 8.93^{ab}	87.95 ± 10.01^{ab}	71.78 ± 8.17^{b}	70.66 ± 8.39^{b}
Prolamin	248.93 ± 26.19^{a}	226.41 ± 24.38^{ab}	203.71 ± 25.75^{b}	181.20 ± 20.05^{bc}	173.63 ± 15.51^{c}	172.46 ± 16.17^{c}
Glutelin	127.56 ± 14.08^{a}	110.07 ± 15.37^{ab}	101.55 ± 13.88^{ab}	101.67 ± 14.05^{ab}	88.78 ± 9.57^{b}	86.36 ± 9.66^{b}

Means sharing the different letter(s) are significantly different ($P < 0.05$)

significantly increased in aCO_2-treated maize plants under Tl contamination (+69–83% for succinate and +32% for lactate). Almost the same results were obtained for citrate content in the grains of both plants under aCO_2, which were significantly greater at 120 mg/kg TI up to 43% in wheat and 56% in maize ($P < 0.05$). Trans-aconitic acid and malate levels in both grains showed minor and non-significant shifts in response to eCO_2 and TI contamination ($P \geq 0.05$). Oxalate concentrations in wheat exhibited a marked increase at 120 mg/kg TI under eCO_2 conditions, while under aCO_2, changes were minimal and non-significant (Table 4).

Table 3. The effect of CO_2 levels and soil thallium (TI) contamination on antioxidant metabolites in the grains of wheat and maize plants

Parameter	Elevated CO_2			Ambient CO_2		
	control	TI (60 mg)	TI (120 mg)	control	TI (60 mg)	TI (120 mg)
Wheat						
Polyphenols (µg GAE/g FW)	545.28 ± 40.28^{c}	650.63 ± 59.76^{b}	873.89 ± 80.65^{a}	566.30 ± 55.18^{bc}	642.29 ± 61.38^{b}	928.39 ± 81.39^{a}
Flavonoids (mg QE/g FW)	83.95 ± 9.11^{a}	83.01 ± 8.67^{a}	84.91 ± 9.23^{a}	90.46 ± 7.79^{a}	95.41 ± 9.38^{a}	101.80 ± 10.16^{a}
Alpha-tocopherols (ng/g DW)	177.72 ± 18.87^{ab}	177.64 ± 19.20^{ab}	215.12 ± 22.22^{a}	154.48 ± 16.16^{b}	187.05 ± 20.18^{ab}	209.19 ± 19.77^{a}
Beta-tocopherols (ng/g DW)	54.87 ± 4.39^{a}	51.28 ± 7.84^{a}	61.07 ± 4.49^{a}	51.34 ± 7.11^{a}	58.51 ± 5.45^{a}	67.29 ± 8.71^{a}
Gamma-tocopherols (ng/g DW)	10.63 ± 1.46^{b}	12.19 ± 1.35^{ab}	13.81 ± 1.19^{ab}	12.02 ± 1.28^{ab}	13.51 ± 1.56^{ab}	15.67 ± 2.06^{a}
Maize						
Polyphenols (µg GAE/g FW)	799.45 ± 87.59^{ab}	926.71 ± 100.04^{a}	869.33 ± 94.07^{ab}	706.59 ± 83.95^{b}	858.15 ± 79.94^{ab}	887.08 ± 90.38^{ab}
Flavonoids (mg QE/g FW)	77.77 ± 8.19^{a}	79.39 ± 7.86^{a}	82.04 ± 9.71^{a}	79.15 ± 8.44^{a}	82.07 ± 9.00^{a}	95.87 ± 10.76^{a}
Alpha-tocopherols (ng/g DW)	164.33 ± 17.32^{b}	223.33 ± 20.39^{a}	237.28 ± 22.29^{a}	132.85 ± 16.38^{b}	223.90 ± 21.20^{a}	225.03 ± 19.57^{a}
Beta-tocopherols (ng/g DW)	72.28 ± 5.59^{a}	63.31 ± 6.79^{a}	72.21 ± 6.98^{a}	65.70 ± 5.89^{a}	64.02 ± 7.14^{a}	71.26 ± 8.03^{a}
Gamma-tocopherols (ng/g DW)	13.63 ± 1.32^{b}	18.45 ± 1.67^{a}	21.14 ± 2.09^{a}	11.93 ± 1.98^{b}	15.29 ± 1.99^{b}	17.98 ± 1.00^{ab}

Means sharing the different letter(s) are significantly different ($P < 0.05$). GAE – gallic acid equivalent; QE – quercetin equivalent; DW – dry weight

DISCUSSION

This study showed the complex interaction between eCO_2, soil Tl contamination, and key physiological parameters in wheat and maize grains. Our findings comprehensively show how these factors influence grain yield and physiological and metabolic responses under different environmental stressors. The grain yield results reveal that both wheat and maize benefit in productivity under eCO_2 conditions compared to ambient CO_2, particularly under moderate Tl contamination levels, highlighting the potential of eCO_2 to alleviate some of the adverse effects of TI. This finding is consistent with previous literature, indicating enhanced crop resilience under elevated atmospheric CO_2 (Alsherif et al. 2023, AbdElgawad et al. 2023). However, the stark decline in yields (around 50% for wheat and 36% for maize) under high Tl contamination (120 mg/kg) underlines the toxicity threshold beyond which the beneficial effects of eCO_2 are overwhelmed by Tl's detrimental impact.

The photosynthesis parameters were studied to determine the physiological mechanisms that underlie the observed changes, as photosynthetic efficiency directly influences crops' overall biomass and grain production. The analysis of photosynthetic pigments underscores differential responses between the two species. Tl's toxicity severely compromises photosynthetic machinery in both plants; however, maize displayed a higher resilience with unchanged Chl *a* content under Tl stress, alongside a dramatic increase (29%) in response to eCO_2. This distinction suggested that, as a C4 plant, maize may possess more effective mechanisms for maintaining chlorophyll synthesis and overall photosynthetic efficiency under heavy metal-induced stress (Srivastava et al. 2012). Carotenoid accumulation increased significantly under the highest Tl contamination in both species, suggesting that these pigments may serve critical antioxidant roles under oxidative stress conditions, thus reinforcing the plants' ability to buffer against Tl toxicity (Albqmi et al. 2023b).

The mineral content analysis reveals nuanced responses to both eCO_2 and Tl levels. Elevated CO_2 enhanced essential nutrient levels such as phosphorus, potassium, and calcium in both crops, supporting improved nutritional quality. However, significant reductions in some nutrients (e.g., phosphorus) under 120 mg/kg Tl highlighted the role of Tl in hindering nutrient availability and uptake under stress conditions (Hrubý et al. 2002). Interestingly, maize exhibited a pronounced ability to maintain calcium levels, with a significant increase observed under high Tl contamination. This resilience suggested that maize might have superior calcium uptake and retention mechanisms, which could help mitigate ionic imbalances (Naz et al. 2024) resulting from Tl exposure, thereby supporting other physiological functions critical for growth. One explanation

Table 4. The effect of CO_2 levels and soil thallium (TI) contamination on organic acids levels (ng/g DW) in the grains of wheat and maize plants

Parameter	Elevated CO_2			Ambient CO_2		
	control	TI (60 mg)	TI (120 mg)	control	TI (60 mg)	TI (120 mg)
Wheat						
Succinate	232.59 ± 25.59^{a}	228.91 ± 28.19^{a}	276.19 ± 31.22^{a}	245.56 ± 25.59^{a}	276.49 ± 28.15^{a}	275.82 ± 30.03^{a}
Malate	63.47 ± 5.59^{a}	65.51 ± 5.55^{a}	74.89 ± 8.92^{a}	70.02 ± 8.01^{a}	73.36 ± 7.34^{a}	80.97 ± 7.89^{a}
Citrate	126.64 ± 14.28^{b}	126.93 ± 12.48^{b}	151.91 ± 24.81^{ab}	134.29 ± 15.27^{b}	149.93 ± 15.09^{ab}	191.92 ± 20.27^{a}
Lactate	135.00 ± 12.22^{a}	120.55 ± 14.94^{a}	121.61 ± 15.03^{a}	145.08 ± 20.23^{a}	128.53 ± 16.43^{a}	143.92 ± 18.49^{a}
Trans-aconitic	26.82 ± 2.54^{a}	23.58 ± 2.22^{a}	21.92 ± 2.68^{a}	27.05 ± 2.43^{a}	25.66 ± 3.11^{a}	24.71 ± 2.34^{a}
Oxalate	38.52 ± 3.34^{b}	41.62 ± 5.43^{ab}	51.44 ± 6.43^{a}	51.14 ± 6.01^{a}	49.46 ± 5.55^{ab}	46.96 ± 5.23^{ab}
Maize						
Succinate	227.64 ± 25.50^{b}	295.61± 30.04^{a}	309.49 ± 21.58^{a}	175.16 ± 24.56^{b}	296.87 ± 31.48^{a}	320.73 ± 25.67^{a}
Malate	77.76 ± 6.45^{a}	87.35 ± 8.16^{a}	85.91 ± 7.94^{a}	73.24 ± 8.11^{a}	77.31 ± 7.96^{a}	79.64 ± 8.59^{a}
Citrate	128.27 ± 18.84^{ab}	169.89 ± 20.03^{a}	161.43 ± 19.53^{a}	99.56 ± 10.04^{b}	111.73 ± 10.54^{b}	174.30 ± 21.22^{a}
Lactate	132.32 ± 16.43^{ab}	121.04 ± 17.43^{ab}	154.62 ± 18.34^{a}	111.57 ± 12.55^{b}	115.08 ± 19.45^{ab}	147.33 ± 17.86^{a}
Trans-aconitic	24.50 ± 3.23^{a}	22.29 ± 3.39^{a}	23.49 ± 2.89^{a}	24.60 ± 3.01^{a}	27.12 ± 3.57^{a}	26.98 ± 3.46^{a}
Oxalate	55.16 ± 6.22^{ab}	53.13 ± 5.61^{ab}	59.37 ± 4.98^{a}	43.34 ± 5.33^{b}	51.12 ± 5.23^{ab}	52.99 ± 5.20^{ab}

Means sharing the different letter(s) are significantly different ($P < 0.05$), DW – dry weight can be the photosynthetic pathway of C4 plants that enhances the concentration of CO_2 (Tian et al. 2024), which may have downstream effects on calcium homeostasis and the management of other vital nutrients. This implies that C4 plants could be more capable of coping with ionic disturbances induced by Tl exposure. Moreover, the dramatic increases in Tl content in wheat and maize under contamination emphasise the critical need for understanding metal bioaccumulation pathways and their potential toxicological impacts. Moreover, the lesser degree of Tl accumulation in maize at the 60 mg/kg level under eCO_2 suggests a beneficial interaction, potentially enhancing antioxidant capacity or detoxification mechanisms within the plant (Riaz et al. 2024).

Then, the present study aimed to analyse soluble sugar and starch content in grains to elucidate how carbohydrate accumulation and metabolism contribute to overall yield and stress resilience under varying conditions of CO_2 and TI contamination. In this regard, the significant increase in total soluble sugars under Tl contamination suggested that both species mobilise carbohydrates as a response mechanism to TI stress. This accumulation of soluble sugars likely serves as an osmotic regulator and energy reserve, vital for maintaining metabolic functions under stress (Afzal et al. 2021, Yaghoubi et al. 2022). Interestingly, while eCO_2 did not appear to alter sugar accumulation directly, it could facilitate broader physiological adaptations leading to increased grain weight and yield through improved overall plant health. A marked reduction in starch content alongside decreased starch synthase activity indicates a metabolic shift towards enhancing sugar synthesis at the expense of starch storage under Tl stress. Coupled with the increased activity of α-amylase, which assists in starch mobilisation, this finding suggests that plants prioritise rapid energy availability to cope with the stress of Tl contamination. It has been reported that the starch content in the grains of stressed plants decreased primarily because they remobilise starch as a source of energy and carbon during stressful conditions to support growth and mitigate stress effects (Thalmann and Santelia 2017). Additionally, numerous studies indicate that starch degradation is a typical response among various plant species, correlating with improved stress tolerance (Thalmann et al. 2016, Wang et al. 2025b).

The subsequent analysis of the amino acid and fatty acid profiles was conducted to investigate how these essential macromolecules influence grain quality, nutritional value, and stress adaptation, thereby providing a comprehensive understanding of the biochemical mechanisms governing crop responses to eCO_2 and TI contamination. Amino acid profiling revealed marked increases in stress-related amino acids like proline and cysteine under Tl contamination. This increase emphasises the role of proline as a protector against oxidative stress and a contributor to osmotic balance under heavy metal stress (Elbasan et al. 2020). The consistent rise in cysteine levels indicates a robust defence mechanism against oxidative damage, aligning with its role in synthesising glutathione and other antioxidants crucial for mitigating stress (Hasanuzzaman et al. 2017). The hierarchical clustering analysis further analysed how the fatty acid profiles were influenced by varying CO_2 and Tl contamination levels. Fatty acids are integral for maintaining membrane integrity and fluidity, particularly in stressful environments, signifying their potential as biomarkers for assessing plant health and resilience within contaminated soils (Upchurch 2008).

The analysis of organic acid contents in grains revealed some variations in response to TI contamination and eCO_2 levels, particularly in maize, which showed a notable increase in succinate and lactate levels under ambient CO_2 conditions. This suggests a potential metabolic adaptation to TI stress. In wheat and maize, citrate levels increased notably under high TI contamination, indicating enhanced organic acid synthesis as part of the plants' stress response under ambient CO_2. However, other organic acids, such as trans-aconitic acid and malate, exhibited non-significant changes across both CO_2 treatments, suggesting that not all organic acid pathways are equally affected by TI stress. These findings underscore the critical role of organic acids in the metabolic adjustment of grains to stress factors, offering valuable insights into the biochemical strategies that crops employ in response to changing environmental conditions.

Despite the insights gained from this study, several limitations must be acknowledged. First, the experimental conditions were conducted in a controlled environment, which may not fully represent the complexities and interactions present in natural field settings, potentially limiting the generalisability of the results across diverse agricultural conditions. Additionally, the limited sampling sizes and the specific concentration levels of TI may have reduced statistical power to detect subtle yet important variations across all measured parameters and the overall impact of CO_2 treatment. Consequently, larger-scale and more comprehensive studies are required to validate our findings and fully understand their implications for crop health and productivity in response to environmental stressors.

In conclusion, this comprehensive study showed that soil TI contamination presented significant challenges to grain yield and quality in wheat and maize, yet elevated CO_2 conditions can foster some resilience by enhancing growth, nutrient absorption, and metabolic adjustments. Future research should continue to explore the underlying molecular and genetic mechanisms that allow these crops to mitigate heavy metal stress while capitalising on the benefits of a changing climate. Understanding these interactions will be vital for developing resilient crop varieties capable of maintaining productivity and quality in an increasingly stressful agricultural landscape.

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