

Exogenous application of Methyl jasmonate alleviates chromium-induced toxicity in *Avena sativa* L. by enhancing the antioxidant defense system and regulating lipid peroxidation

Salim Salim Salim

Chaudhary Charan Singh University

Shivani Chauhan Shivani Chauhan

Chaudhary Charan Singh University

Rajesh Pareek Pareek

Chaudhary Charan Singh University

Ishwar Singh Ishwar Singh

www.ishwarsingh@gmail.com

Chaudhary Charan Singh University

Research Article

Keywords: Chromium toxicity, Antioxidants, Malondialdehyde content, Methyl Jasmonate, Sustainable agriculture

Posted Date: February 26th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-8828963/v1>

License:   This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Additional Declarations: No competing interests reported.

Exogenous application of Methyl jasmonate alleviates chromium-induced toxicity in *Avena sativa* L. by enhancing the antioxidant defense system and regulating lipid peroxidation

Salim Salim¹, Shivani Chauhan¹, Rajesh Pareek¹, Ishwar Singh^{1*}

¹Phytochemistry & Metabolic Studies Laboratory, Department of Botany, Chaudhary Charan Singh University, Meerut, Uttar Pradesh-250001, India.

Corresponding author email: www.ishwarsingh@gmail.com

Orcid ID - <https://orcid.org/0000-0001-6251-4419>

Abstract

High levels of hazardous metals such as chromium (Cr) have been produced over decades of growing industrial activity, which reduces crop productivity. The impact of Cr on the physio-biochemical characteristics of *A. sativa* L. was assessed in this study. It was further shown that exogenous application of MeJA mitigated Cr-induced toxicity. The performance of oats was first assessed by measuring growth parameters (Plant Shoot length, root length, and biomass) and physio-biochemical parameters (Enzymatic and Non-enzymatic antioxidants). This study examined how methyl jasmonate (MeJA 50 and 100 μ M) reduced Cr stress at concentrations of 50, 100, and 150 μ M. The findings demonstrated that Cr stress drastically decreased photosynthetic pigments, protein content, and total carbohydrate content accumulation in the leaves, which in turn decreased the biomass and height of plants. In addition to inducing oxidative stress and raising leaf levels of oxidative stress markers, chromium toxicity was linked to elevated malondialdehyde levels by 44.70% compared to the control. However, in plants under Cr stress, MeJA supplementation enhanced the amounts of photosynthetic pigments, decreased the Cr accumulation in plants, and enhanced the efficiency of the photosynthetic machinery. By upregulating antioxidant enzymes, MeJA supplementation improved the antioxidant defense system, including POD (+127%) at 150 mM Cr + 100 μ M MeJA, CAT at 150 μ M Cr + 100 μ M MeJA (+93% vs. control), and SOD (+82.9%) at 150 μ M Cr + 50 μ M MeJA. By lowering the MDA content by 44.70% and 25.37%, respectively, MeJA application also reduced lipid peroxidation (E1 and E2). MeJA at a concentration of 100 μ M was found to be more effective in reducing Cr toxicity. Consequently, MeJA supplementation might be a practical way to reduce Cr absorption and its negative effects on plants of the *A. sativa* L. grown in environments contaminated with Cr.

Keywords: Chromium toxicity, Antioxidants, Malondialdehyde content, Methyl Jasmonate, Sustainable agriculture.

Acknowledgment

The authors sincerely thank the CSIR- (UGC) University Grant Commission for financial support. Additionally, we acknowledge the Department of Botany, Chaudhary Charan Singh University, Meerut (U.P.) India.

Conflict of interest

The authors declare that they have no conflict of interest.

Introduction

Heavy metal contamination in the soil has raised concern to the environment and human beings. The buildup of these metals poses significant threats to both human health and agricultural output. Various factors contribute to their release into the environment, with human activities such as mining operations, pesticide application, and industrial waste discharge being major sources (Ali et al., 2024; Gupta et al., 2024; Wang et al., 2024). Rapid industrial growth and inadequate industrial waste management are the main causes of heavy metal pollution, one of the world's most significant environmental issues. This makes farmland more contaminated with HM. Wang and Chen (2009) state that HMs typically enter the food chain by being absorbed and accumulated by plants, which are then consumed by end users and can result in a variety of health problems. One of the heavy metals (HMs) that seriously contaminates soil, sediment, and groundwater globally is chromium (Cr) (Diwan et al., 2010). Cr compounds are released into the environment by a variety of industries through gaseous emissions, wastewater, and waste. Fertilizers or waste products meant for soil improvement introduce large amounts of chromium into the soil (Ghosh et al. 2003; Dampare et al. 2006; Shams et al. 2010). Water bodies and surrounding areas of the Hindon River, an Indian tributary of the Yamuna River, have been found to be contaminated with chromium. Without adequate pre-treatment, industrial wastewater from Ghaziabad City enters the Hindon River. The use of this contaminated Hindon River water for irrigation in neighboring agricultural fields affects the quality of the vegetables and cereals grown under these conditions (Singh et al., 2020). This issue affects people all over the world. It is still unclear how exactly chromium is absorbed and moved through plants. Plants need energy and active phosphate and sulfate transporters to absorb hexavalent (Cr VI) chromium through the plasma membrane (Ali et al., 2023). Chromium poisoning of plants produces a variety of Reactive Oxygen Species (ROS), including O_2^- , H_2O_2 , and OH^- radicals. The elevated activity of ROS damages cellular components such as proteins, lipids, and nucleic acids (Daud et al., 2021). Because of oxidative reactions that harm DNA and RNA, lipid peroxidation, protein oxidation, and enzyme inhibition, high ROS levels can kill cells (Srivastava et al., 2021).

Plants have also evolved a number of complex adaptation strategies to regulate the high levels of reactive oxygen species (ROS) produced in response to biotic and abiotic stressors, such as chelation by organic compounds followed by vacuole storage (Azeez et al., 2021; Pushkar et al., 2021). Plants also have a secondary system for generating antioxidant enzymes to counteract the elevated levels of Cr-induced ROS (Srivastava et al., 2021; Ao et al., 2022). It is crucial for investigating chromium uptake in soil-plant systems and potential ecological issues related to elevated chromium levels. In light of HM toxicity, various research has been done to find a cost-effective and sustainable way to increase plant growth and productivity (Ghorbani et al., 2022). It has been discovered that phytohormones are cost effective and efficient to increase plant resistance to heavy metal toxicity, including chromium (Kamran et al., 2021).

Among many other functions, methyl jasmonate (MJ) is a signaling molecule that can regulate growth and development, trigger defense mechanisms in plants, and interact with different plant hormones (Mir et al., 2018). Changes in MJ levels have been shown to enhance a plant's resistance to environmental stressors (Najafi Kakavand et al., 2019; Mir et al., 2018). Exogenous MJ treatment has been shown to effectively increase the synthesis of osmoregulatory molecules and boost the antioxidant defense system, potentially increasing plant stress tolerance (Mousavi et al., 2020; Farhangi-abriz and Ghassemi-golezani, 2018). Previous research suggests that MJ applied externally helps plants adapt to a variety of stressors, including arsenic (Mousavi et al., 2020), cadmium (Yan et

al., 2015), salinity (Farhangi-abriz and Ghassemi-golezani, 2018), and drought (Alam et al., 2014). However, little is known about the exact mechanism by which MJ triggers the plant's defenses against chromium toxicity.

Oats (*Avena sativa* L.), an important cereal crop grown largely in temperate countries for human consumption and animal feed, are members of the Poaceae plant family. By 2024, approximately 22 million tonnes of oats will be produced globally, with an average yield of 2.6 tonnes per hectare farmed on 8.7 million hectares (FAO, 2024). The top producers, Canada and Russia, each contribute roughly 3.9 million tonnes annually, with Poland, Australia, Brazil, and the United States coming in second and third, respectively (USDA Foreign Agricultural Service, 2023). Due to rising consumer demand for plant-based and gluten-free options, the global oat market is expected to reach USD 8.2 billion by 2030 from its estimated USD 6.6 billion in 2022 (IndexBox, 2024). Oats are farmed on around 0.25 million hectares of land in northern, central, and eastern India as a rabi (winter) fodder crop. Punjab, Haryana, Uttar Pradesh, Madhya Pradesh, Bihar, and several northeastern and hilly regions are key oat-growing states (ICAR-IGFRI, 2015). Despite its tiny national production, oat output has consistently increased in recent years, owing to increased interest, particularly in smallholder farming practices and animal nutrition (ICAR, 2023-2024). Despite increased prospects for human consumption aligned with global trends, the crop is yet to acquire traction as a staple food in India (The Economic Times, 2023). Previous studies have shown that both trivalent chromium (Cr (III)) and hexavalent chromium (Cr (VI)) significantly impair oat growth and biochemical activity. In hydroponic and soil-based pot experiments, Cr (III), especially Cr (VI), significantly lowers oat biomass, affecting both the aboveground and root sections. Cr (VI) is especially damaging, preventing germination at concentrations of 100 mg/kg soil or above (Wyszkowski & Radziemska, 2010; Szopińska et al., 2019). According to Zhao et al. (2019), chromium toxicity hinders plant development and yield, interferes with metabolic processes, and reduces the availability of essential minerals such as calcium, iron, manganese, copper, zinc, and salt. Chromium toxicity and tolerance vary depending on crop type and growth stage.

Materials & Methods

Plant material and growth conditions

Oat (*Avena sativa* L.) var JHO 2015 was used as experimental material. Seeds were gathered from the Indian Grassland and Fodder Research Institute (IGFRI), located at ICAR in Jhansi, Uttar Pradesh, 284 003, India. For the current investigation, seeds of the same size were chosen. During the rabi season of 2024-2025, the experiment was carried out in 27 earthen pots at the experimental site at the Botany department of CCS University, UP. Eight kilograms of pre-sterilized sandy loam soil from the experimental site were put into the pots. In September 2024, the healthy seeds were sown in the pots.

Seed viability test:

The seed's viability was assessed using the tetrazolium test. The seed's surface was sterilized for ten minutes using mercuric chloride (HgCl_2) in a 0.2 percent aqueous solution. After that, they were carefully cleaned with running tap water. Following sterilization and washing, seeds were submerged in running tap water at 25 to 20 degrees Celsius for a full day. After that, the embryos were gathered and left in TzCl_2 for a full day without light. Red or pink-dyed embryos were regarded as viable. Usually, the data were presented as a viability percentage.

Sterilization and sowing of seeds:

After being surface sterilized for ten minutes with a 0.2% mercuric chloride (HgCl₂) solution, the mustard seeds were cleaned with distilled water and allowed to soak. The seeds were soaked for a full day before being planted in pots to test for germination. utilizing (K₂Cr₂O₇) as the Cr source. To observe their germination, three treatments with varying concentrations (50, 100, and 150 µM Cr) and/or MJ (50, 100 µM) were employed; the control was tap water. Ten seeds per pot were sown at 25 ± 2 °C, which is field-like conditions. Three duplicates of each treatment were used.

Growth parameters

On chart paper, plant material was collected and measured. The height of the plant roots and shoots was measured with a measuring scale, and their weight was measured with a weighing balance. A digital weighing balance was used to measure the fresh weight, dry weight, moisture percentage, and content of air-dried plants after they had been in the vegetative stage for 45 days. They were put in small paper envelopes with clear labels before going into the oven. Before being weighed, the plants were dried for 48 hours at 60°C.

Biochemical Analysis

Chlorophyll Content Estimation (Arnon, 1949):

50 mL of freshly crushed leaves were ground in 10 mL of 80% acetone. After that, it was centrifuged at 5000–10,000 rpm for 5 minutes. After the supernatant was transferred, the same procedure was carried out again until the residue had lost its color. At 645 and 663 nm, the absorbance of the solution was measured in comparison to a blank (80% acetone). The concentrations of chlorophyll were estimated using the following formula:

$$\text{Total Chl. (mg/g. f. wt.)} = \frac{20.2 (A_{663}) + 8.02 (B_{645}) \times V}{1000 \times W}$$

Determination of Protein Content

To determine the protein content, 100 mg of fresh leaf tissue was homogenized in 5.0 ml of TrisHCl buffer (pH 7.0) and centrifuged for 10 minutes at 10,000 rpm. Absorbance at 595 nm was measured after 1.0 ml of sample extract was mixed with 5.0 ml of Coomassie brilliant blue dye (Bradford, 1976).

Detection of Proline Content

The proline content was estimated using the Bates et al. (1973) method. After collecting fresh 0.5 g samples of root and shoot tissue, they were homogenized in 3% aqueous sulphosalicylic acid and filtered through Whatman filter paper (Praxor, Tamil Nadu, India). 4 mL of toluene was used to extract the filtered extract after it had been combined with 2 mL of glacial acetic acid and 2 mL of ninhydrin and boiled for an hour at 100 °C in a water bath. To determine the proline content, the absorbance of the chromophore phase at 520 nm was measured using a Shimadzu Corp. 2600 UV Spectrometer in Kyoto, Japan. The amount of proline was expressed as µM g⁻¹ fresh weight (FW).

Malondialdehyde (MDA) Content

The MDA content of tissues (roots and shoots) was measured using Heath and Packer's (1968) method. Fresh root and shoot samples (approximately 0.25 g each) were homogenized with 2 mL of 0.1% trichloroacetic acid, and then they were centrifuged at $10,000 \times g$ for 10 minutes. The mixture was incubated for 30 minutes at 95°C in hot water after 1 mL of the supernatant was added to 4 mL of 0.5% thiobarbituric acid in 20% trichloroethanoic acid. The reaction was stopped on ice and then centrifuged at $10,000 \times g$ for 30 minutes. At 532 and 600 nm, the supernatant's absorbance was measured. Using an absorbance coefficient of extinction of $155 \text{ mM}^{-1} \text{ cm}^{-1}$, the MDA contents were calculated by subtracting the nonspecific absorption at 600 nm from the absorption at 532 nm.

Estimation of Carbohydrate Content

Sugar was extracted using the Anthrone reagent (McCready et al. 1950). Using a water bath, 0.5 mg of ground dried leaf samples were boiled for 30 minutes in 10 mL of 80% ethanol. The homogenate was centrifuged for five minutes at 4000 rpm after being allowed to cool to room temperature. The supernatant from the three extraction rounds was combined to estimate the amount of sugar. One milliliter of the supernatant and four milliliters of Anthrone reagent were heated to a boil for ten minutes in a water bath. The absorbance at 620 nm was measured with a Shimadzu (UV-2600, Japan), and glucose standard solutions were used to estimate the sugar concentration.

Estimation of Total Phenolic Content (TPC)

The Bray and Thorpe (1954) method was used to estimate phenolics. In a mortar and pestle, 50 mg of plant tissue was mixed with 5 mL of 80% ethanol before being centrifuged at 5000 rpm. After collecting the supernatant, 2.5 mL of 80% ethanol was used to reextract the pellet. After the pooled supernatants were dried out by evaporation, the residue was dissolved in five mL of distilled water. After reacting with 0.5 mL of phenol reagent, 2.0 mL of 20% Na_2CO_3 was added to the aliquot. At 650 nm, absorbance was measured, and a gallic acid calibration curve was employed for computation.

Total Nitrogen Content

50 mg of plant material was digested using 2.0 mL of 30% H_2O_2 and 5.0 mL of concentrated H_2SO_4 (Snell & Snell, 1949). For 30 minutes, the boiling test tubes were placed on a hot plate (sand bath) to aid in digestion. 3.0 mL of 30% H_2O_2 was once more added to the test tubes that had been allowed to cool to room temperature. The tubes were then allowed to digest for an additional sixty minutes, or until the digest turned transparent. The color that developed at 425 nm was measured after 1.0 mL of the digest, 3.0 mL of Nessler's reagent, and 1.0 mL of distilled water were combined. A 0.5M $(\text{NH}_4)_2\text{SO}_4$ standard solution was made for the nitrogen standard curve. The test tubes holding 3.0 mL of this solution were filled with 0.1 to 1.0 mL. The nitrogen content was calculated and expressed as N%.

Determination of antioxidant enzyme activity

Forty-five days after seeding, fresh leaf samples were taken from the uppermost portion of the plant to determine the amount of enzymatic antioxidants. A Shimadzu 2600 UV Spectrometer was used to spectrophotometrically

measure the activity of the antioxidant enzymes, specifically SOD, POD, and CAT. Using a pre-cooled mortar and pestle, 1.0 g of leaf samples were thoroughly crushed. They were then homogenized in 10 mL of 0.05 M phosphate buffer (pH 7.8), filtered through muslin cloth, and centrifuged at $10,000 \times g$ for 15 minutes at 4 °C. SOD and POD activity were then measured using the enzyme extract and the Maehly & Chance (1954) method. CAT activity was measured in compliance with Aebi (1984). 50 mM phosphate buffer (2.8 mL, pH 7.0) containing 2 mM Ca, 300 mM H₂O₂ (100 µL), and enzyme extract (100 µL) were included in the assay samples (3 mL). CAT activity was then determined by measuring the decrease in absorbance at 240 nm brought on by H₂O₂. APX activity was measured using Nakano and Asada's (1981) methodology. APX activity was determined by monitoring the change in absorbance at 290 nm.

Statistical analysis

Protein content, proline concentration, carbohydrates, starch, total nitrogen content, total phenolic content, photosynthetic pigments (carotenoid and chlorophyll), and antioxidant enzymes (SOD, CAT, and POD) were measured in triplicate for each experiment. Pearson's product-moment correlation was used to assess the relationships between physiological and biochemical parameters using RStudio (v4.2.3) at significance levels of $p \leq 0.05$ and $p < 0.01$. Significant differences between treatment groups were evaluated using a one-way ANOVA, and multiple comparisons were evaluated using Tukey's Honestly Significant Difference (HSD) test ($p \leq 0.05$). Principal Component Analysis (PCA) is used to visualize the overall data structure and find trends of variation and clustering among the treatments.

Results

Growth Characteristics

Effect on Plant height:

Shoot and root lengths were measured as 100% in control plants. In comparison to the control, the application of methyl jasmonate alone resulted in improved growth, with shoot length reaching 101.08% (C+E1) and 104.16% (C+E2), and root length reaching 99.23% (C+E1) and 102.97% (C+E2). Both parameters clearly declined in a dose-dependent manner after being exposed to chromium stress. Shoot and root lengths decreased to 89.60% and 80.55%, respectively, at 50 µM Cr (**Fig. 1,2,3**). Additional decreases were noted at 100 µM Cr (83.37% shoot and 75.82% root), but the greatest inhibition was at 150 µM Cr (T3), where the length of the shoot dropped to 78.69% and the length of the root to 61.54% of the control. Supplementing with methyl jasmonate, however, significantly reduced these decreases. While root length nearly fully recovered to 98.90% (T1+E1) and 98.57% (T1+E2) at T1, shoot length recovered to 91.57% (T1+E1) and 94.20% (T1+E2). MeJA also increased the length of the roots to 93.41% (T2+E1) and 84.29% (T2+E2), and the shoots to 87.98% (T2+E1) and 92.25% (T2+E2) at T2. MeJA increased shoot length from 78.69% to 86.13% (T3+E1) and 90.91% (T3+E2) and root length from 61.54% to 86.04% (T3+E1) and 87.91% (T3+E2), even under the highest chromium stress (T3, 150 µM). On the other hand, exogenous methyl jasmonate, especially at 100 µM (E2), significantly reduced growth inhibition and maintained both shoot and root development throughout, whereas chromium stress significantly decreased shoot and root growth in a concentration-dependent manner overall.



Fig. 1. *Avena sativa* L. plants grown under Cr with or without MeJA (A. 30-day-old plants, B. 45-day-old plants).

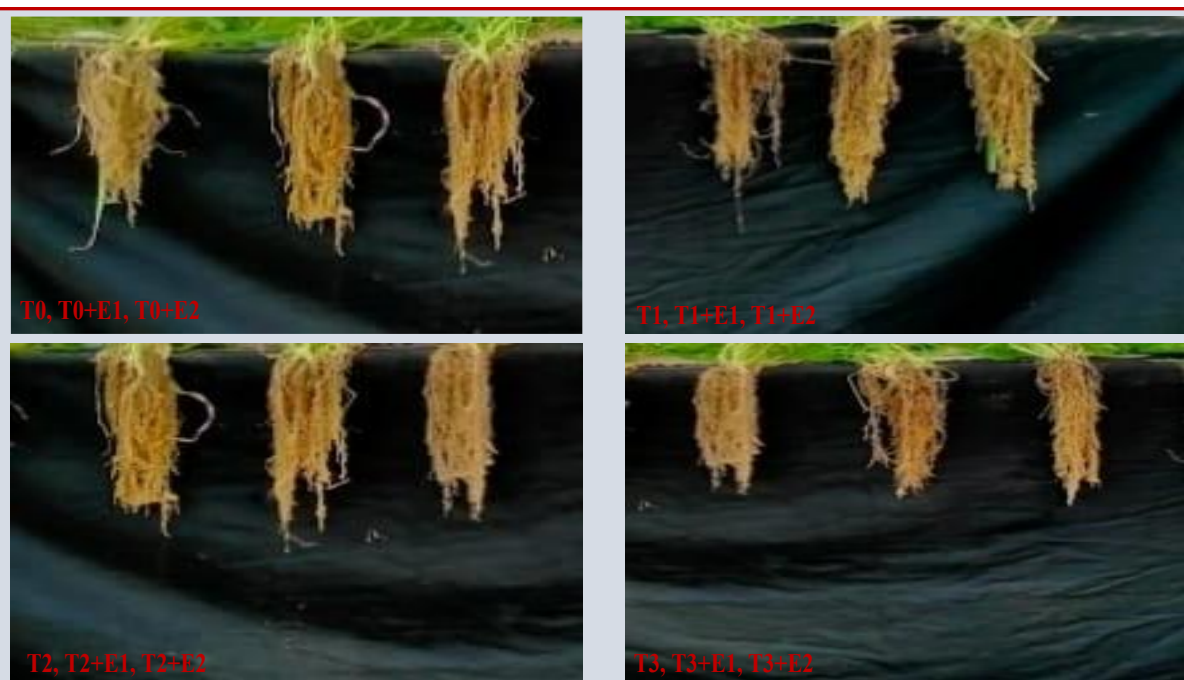


Fig. 2: Showing the effect of different concentrations of Cr and MeJA on Avena roots (T0, T1, and T3 are showing Control without Cr, T1 and T2 are 50 and 100 mM Cr concentrations, E1 and E2 are 50 and 100 μ M MeJA concentrations.

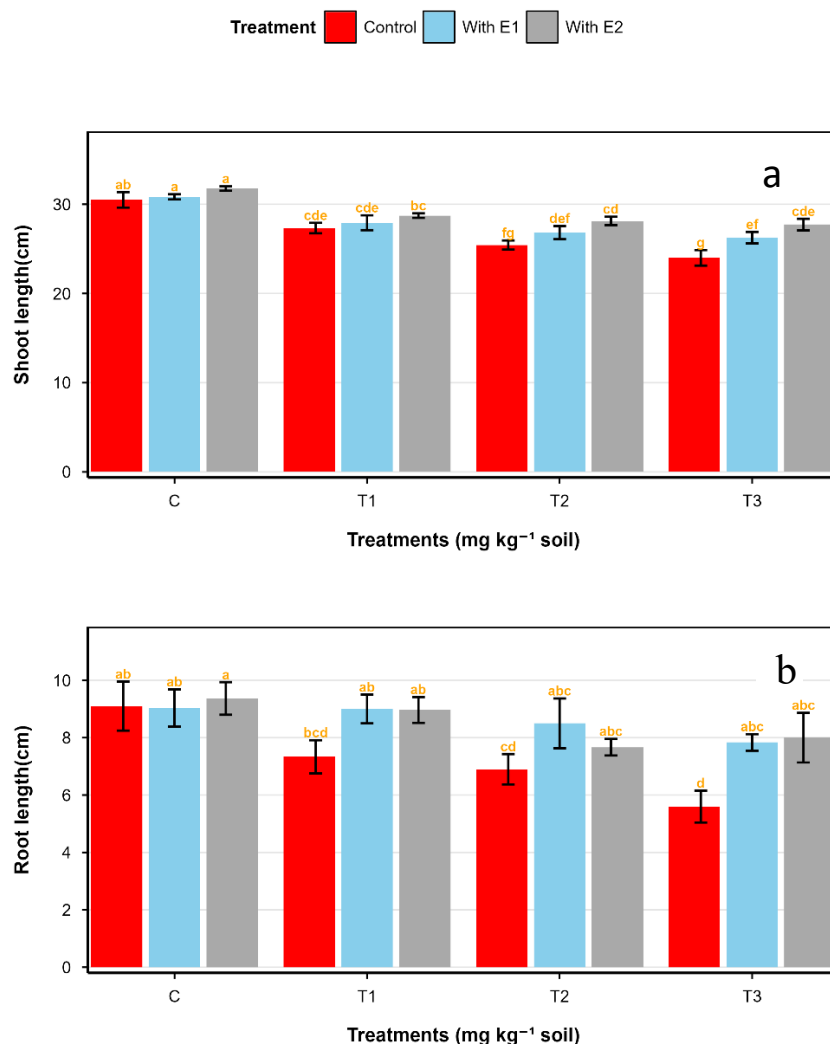


Figure 3: Showing the effect of different concentrations of Cr (50, 100, and 150 µM) with or without MeJA (50, 100 µM) on plant height. a) effect on Shoot, b) effect on Root length.

Effect on Plant Biomass

The fresh weight of the control plants was 5.80 g (100%), and the dry weight was 0.645 g (100%). Applying methyl jasmonate in a non-stressed environment increased biomass; fresh weight increased to 105.21% (C+E1) and 111.21% (C+E2), while dry weight increased to 134.57% (C+E1) and 147.91% (C+E2). Both parameters significantly decreased under chromium stress in a concentration-dependent manner as shown in (Fig. 4a, b). The most severe inhibition was seen at 150 µM Cr (T3), where biomass decreased to 56.72% (FW) and 57.21% (DW) of the control. Fresh weight dropped to 75.87% and dry weight to 63.72% at 50 µM Cr (T1), and values further decreased to 72.41% (FW) and 62.33% (DW) at 100 M Cr (T2).

Cr-induced reductions were considerably lessened by the exogenous administration of methyl jasmonate. At T1, fresh weight increased to 84.11% (T1+E1) and 98.97% (T1+E2) after supplementation, and dry weight increased to 90.70% (T1+E1) and 89.77% (T1+E2). Fresh weight also increased to 93.62% (T2+E1) and 84.83% (T2+E2) under T2 stress, while dry weight increased to 89.60% (T2+E1) and 83.57% (T2+E2). MeJA supplementation

increased fresh weight from 56.72% to 86.03% (T3+E1) and 81.72% (T3+E2), as well as dry weight from 57.21% to 94.57% (T3+E1) and 81.40% (T3+E2), even at the highest chromium level (T3). Both fresh and dry biomass were thus severely suppressed by chromium stress; however, exogenous methyl jasmonate, especially at 100 μ M (E2), significantly reduced growth inhibition and preserved plant productivity.

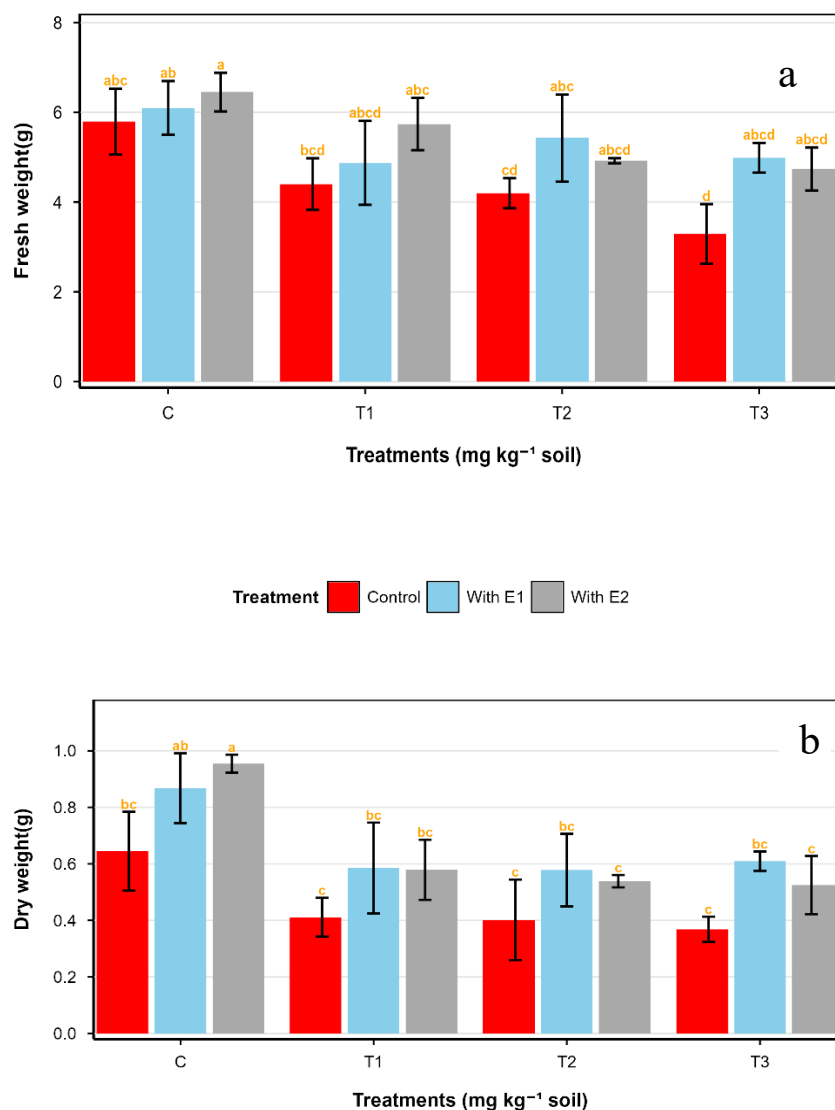


Figure 4: Showing the effect of different concentrations of Cr (50, 100, and 150 μ M) with or without MeJA (50, 100 μ M) on plant Biomass. a) effect on Fresh weight, b) effect on Dry weight. Data are presented as mean $\pm$ SD (n = 3). Significant differences among treatments were determined by one-way ANOVA followed by Tukey's HSD test ($P \leq 0.05$), indicated by different letters (a-f).

Effect on Photosynthetic Pigments

In comparison to the control, the chlorophyll content gradually decreased as the chromium stress increased, going from mild stress at T1 (-12.83%) to severe stress at T3 (-31.13%). Under Cr stress, carotenoids also exhibited a

declining trend, with T3 causing the biggest decrease (-24.47%), as shown in **(Fig. 5a)**. This suggests that chromium hinders the synthesis of photosynthetic pigments by causing oxidative stress.

To varying degrees, MeJA supplementation (50 μ M, 100 μ M) reduced pigment loss. 100 μ M MeJA significantly increased carotenoids (+17.61%) and nearly completely restored chlorophyll (+1.46%) under mild Cr stress (T1). 100 μ M MeJA once more enhanced both pigments (carotenoids +14.50%, chlorophyll -10.07%) under moderate stress (T2), whereas E1 had only modest effects as shown in **(Fig. 5b)**. Both E1 and E2 reduced pigment loss under extreme Cr stress (T3), with E1 improving carotenoids more (+10.32%) and E2 restoring chlorophyll a little better (-10.63%). It's interesting to note that MeJA at higher concentrations (E2, 100 μ M) protected carotenoids from chromium stress more effectively than E1 (50 μ M). According to these findings, MeJA can maintain photosynthetic capacity and partially reverse oxidative damage caused by chromium, with effectiveness varying according to the degree of Cr stress and MeJA dosage.

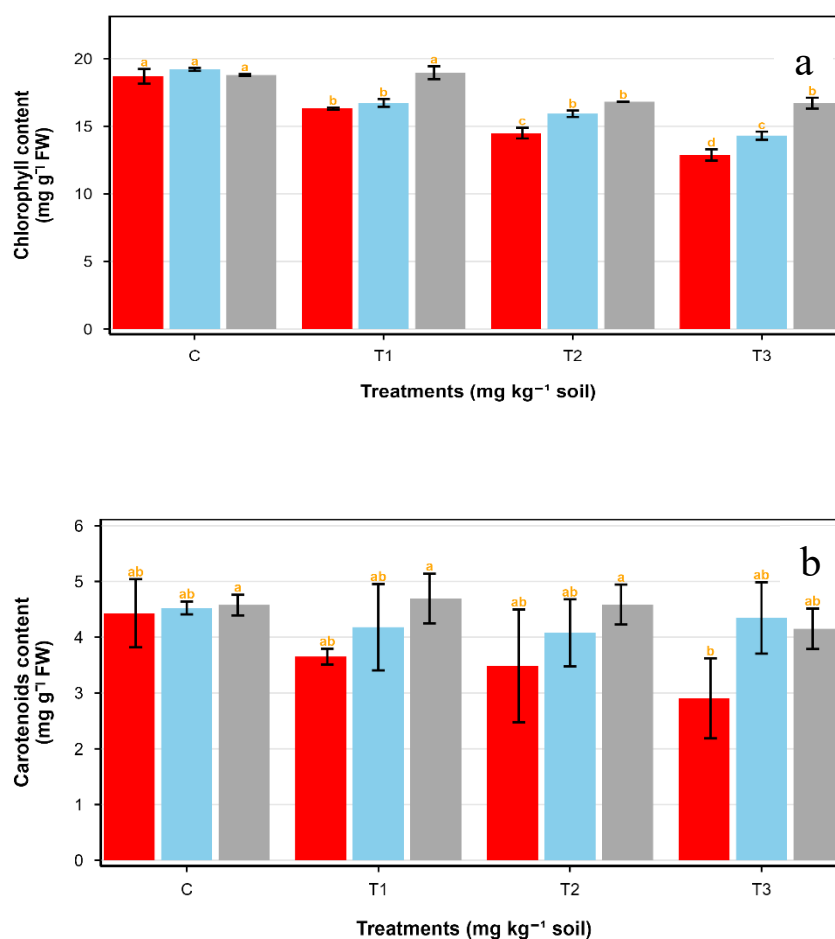


Figure 5: Showing the effect of different concentrations of Cr (50, 100, and 150 μ M) with or without MeJA (50, 100 μ M) on Photosynthetic pigments. a) effect on Total Chlorophyll content. b) effect on Carotenoid content. Data are presented as mean $\pm$ SD (n = 3). Significant differences among treatments were determined by one-way ANOVA followed by Tukey's HSD test ($P \leq 0.05$), indicated by different letters (a-f).

Effect on Soluble Protein Content

Under chromium stress, protein content followed the patterns of carotenoids and chlorophyll. Protein levels decreased gradually as a result of chromium treatments, going from mild stress at T1 (-27.20%) to severe stress at T3 (-46.85%). Some losses were lessened by co-application with 50 and 100 μ M MeJA. For instance, T3+E2 reduced the severe Cr-induced decline to -29.79%, while C+E1 slightly enhanced protein (+7.86%), as shown in (Fig. 6a). Under Cr stress, E2 (100 μ M MeJA) continuously enhanced photosynthetic pigments and protein, indicating its protective function in maintaining plant metabolic processes.

Effect on Proline Content

Proline content estimation revealed that the plant's proline content rose in tandem with the Cr concentration. For the control plants (C), the average value was 6.95. Regarding this, the treatments showed increasing levels over time. Applying methyl jasmonate by itself raised the control by 4.37% (C + E2) and 1.41% (C + E1). The value increased by 6.74% when chromium was added at 50 mM (T1), and then by 10.38% and 10.69% when methyl jasmonate was added at 50 μ M and 100 μ M (T1 + E1 and T1 + E2) respectively. When paired with E1 and E2, the proline content increased to 17.25% at 100 μ M Cr (T2), then to 23.28% and 27.34%. At concentrations below 150 μ M Cr (T3), the greatest responses were observed, exhibiting a 33.45% increase over the control, as shown in (Fig. 6b). This was further increased to 37.22% and 38.18% with the application of E1 and E2, respectively. These results demonstrate that methyl jasmonate dose-dependently amplifies the effects of chromium stress.

Effect on Malondialdehyde (MDA) Content

The mean MDA content of the control plants (C) was 6.27. In contrast, MDA was marginally decreased by methyl jasmonate alone by 3.62% (C + E1) and 3.89% (C + E2). With 50 μ M methyl jasmonate (T1 + E1 and T1 + E2), the 14.23% increase in chromium at 50 μ M (T1) was moderated to 9.80% and 8.46%. MDA rose 19.19% at 100 mM Cr (T2), but the addition of E1 and E2 decreased MDA to 6.85% and 4.56%, respectively. At 150 μ M Cr (T3), the greatest MDA accumulation was seen, with a striking 66.85% increase over control; E1 and E2 reduced this to 44.70% and 25.37%, respectively, as shown in (Fig. 6c). These results show that methyl jasmonate efficiently and dose-dependently reduces Cr-induced lipid peroxidation.

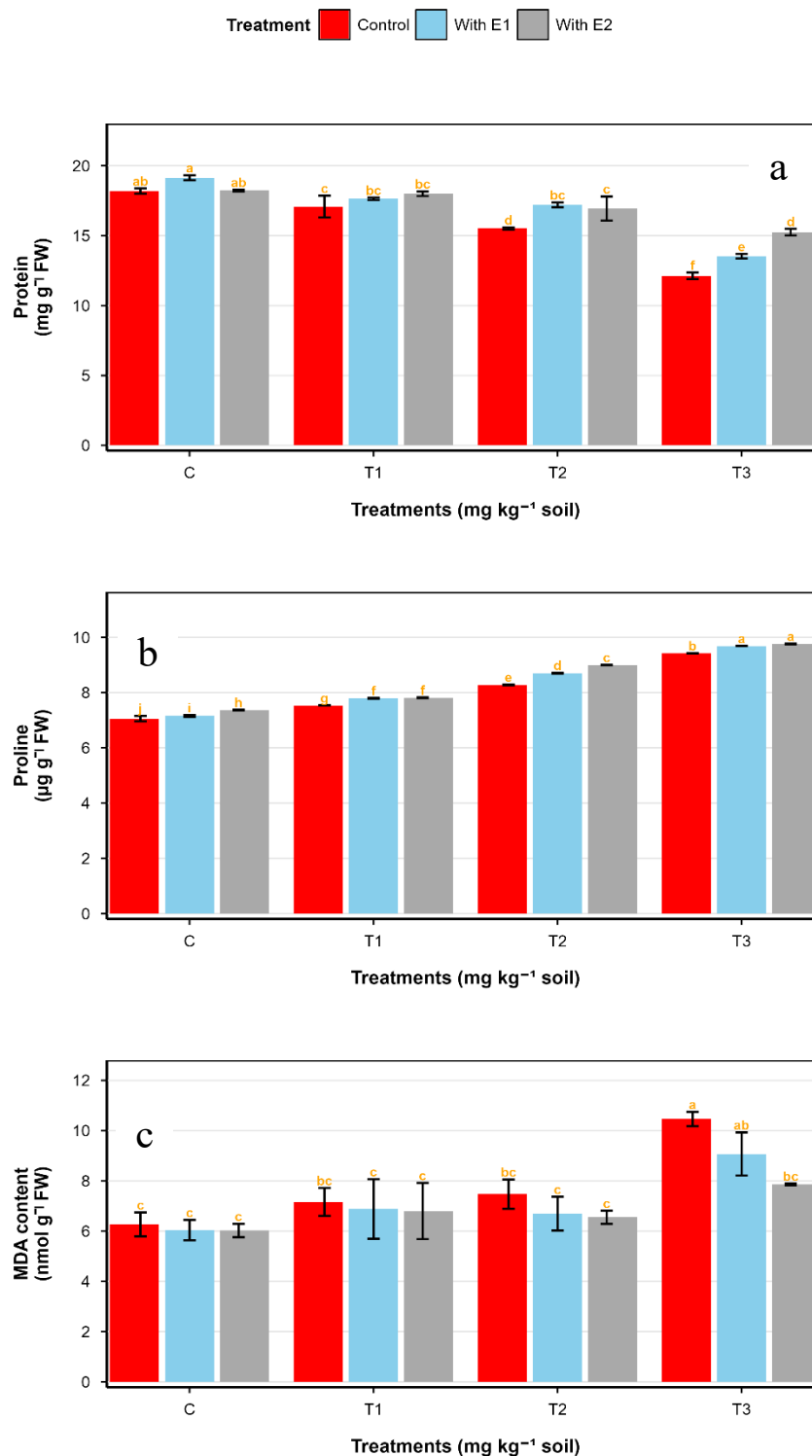


Figure 6: Showing the effect of different concentrations of Cr (50, 100, and 150 μ M) with or without MeJA (50, 100 μ M) on plant biochemical attributes. a) effect on Protein content, b) effect on Proline content. c) effect on lipid Malondialdehyde content. Data are presented as mean $\pm$ SD (n = 3). Significant differences among treatments were determined by one-way ANOVA followed by Tukey's HSD test ($P \leq 0.05$), indicated by different letters (a-f).

Effect on Carbohydrate Content

The chromium (Cr)-induced decrease in plant carbohydrate content was significantly mitigated by the application of methyl jasmonate (MeJA). The average carbohydrate content under control was 22.95 units; after applying MeJA, this amount increased by 2.15% at 50 μM (E1) and 4.36% at 100 μM (E2) MeJA, respectively. Chromium stress exposure dramatically decreased the accumulation of carbohydrates, with declines of 10.19%, 24.20%, and 39.54% noted under 50 μM (T1), 100 μM (T2), and 150 μM (T3) Cr treatments, respectively. Nevertheless, these decreases were significantly lessened by the exogenous administration of MeJA. Treatment with 100 μM MeJA (E2) decreased the decline from 10.19% to 8.79% at 50 μM Cr (T1). Under 100 μM Cr (T2), a greater protective effect was seen, as the decline dropped from 24.20% to just 0.67% with E2. Likewise, in the presence of 100 μM MeJA, the reduction was mitigated from 39.44% to 9.23% under extreme stress conditions (150 μM Cr, T3). These results unequivocally show that MeJA contributes significantly to the preservation of carbohydrate homeostasis under Cr stress, most likely by stabilizing cellular metabolism, enhancing antioxidant defense systems, and activating stress-responsive genes, as shown in (Fig. 7a).

Effect on Total Phenolic Content (TPC)

Both the methyl jasmonate (MeJA) and chromium (Cr) treatments resulted in a noticeable and consistent increase in the total phenolic content when compared to the untreated control (C). At 27.92 mg g^{-1} FW, the control had the lowest mean value. Phenolic accumulation increased to 34.13, 40.45, and 38.29 mg g^{-1} FW upon exposure to Cr at 50 μM , 100 μM , and 150 μM . These increases corresponded to increases of 22.2%, 44.9%, and 37.1%, respectively, suggesting a strong dose-dependent induction up to 100 μM Cr and a slight decline at 150 μM . MeJA improved this response even more. Phenolic content increased to 34.99, 43.60, and 42.35 mg g^{-1} FW in T1, T2, and T3 at the lower MeJA dose (E1, 50 μM), which corresponded to increases of 25.4%, 56.2%, and 51.7% over control. The same Cr treatments produced 38.56, 38.29, and 39.87 mg g^{-1} FW at the higher MeJA dose (E2, 100 μM), indicating increases of 38.1%, 37.1%, and 42.8%, respectively, as shown in (Fig. 7b). T2 + E1 (100 μM Cr + 50 μM MeJA) showed the biggest improvement, rising by about 56% in comparison to the control. MeJA supplementation raised phenolics even in control conditions; C + E1 and C + E2 recorded 29.33 and 30.80 mg g^{-1} FW, respectively, which is 5.1% and 10.3% higher than control. In contrast to higher MeJA levels or excessive Cr, these results show that moderate Cr stress (100 μM) strongly stimulates phenolic biosynthesis and that co-application of a lower MeJA dose synergistically amplifies this response.

Effect on Total Nitrogen Content (TNC)

In comparison to the untreated Plants (47.06 mg g^{-1} FW), the nitrogen content gradually decreased as the chromium (Cr) concentration increased, suggesting a significant inhibitory effect of Cr on nitrogen assimilation. Methyl jasmonate (MeJA) with control showed modest improvements, with C + E1 and C + E2 recording 48.46 and 49.73 mg g^{-1} FW, respectively, which is 2.98% and 5.67% higher than the control. On the other hand, nitrogen content decreased to 41.93, 35.49, and 27.96 mg g^{-1} FW after exposure to Cr at 50, 100, and 150 μM (T1, T2, and T3), indicating decreases of 10.88%, 24.58%, and 40.58%, respectively, indicating a dose-dependent inhibition. These losses were reduced at all Cr levels by the use of MeJA. E1 and E2 supplementation increased nitrogen levels to 44.13 and 45.93 mg g^{-1} FW at 50 μM Cr, respectively, limiting the reduction to 6.23% and 2.41%. Similarly, at 100 μM Cr, the nitrogen content decreased by 24.58%, but the E1 and E2 treatments increased it to

41.46 and 41.56 mg g⁻¹ FW, reducing the decline to about 11.8%. MeJA supplementation provided considerable protection even at the highest Cr concentration (150 μ M): T3 + E1 and T3 + E2 kept nitrogen at 31.39 and 38.86 mg g⁻¹ FW, which corresponded to 33.25% and 17.42% decreases, respectively, in comparison to the control. Overall, these results demonstrate that chromium stress causes a marked, concentration-dependent decline in nitrogen content, but co-application of MeJA, particularly at the higher dose (100 μ M), substantially mitigates this negative impact, as shown in **Fig. 7c**.

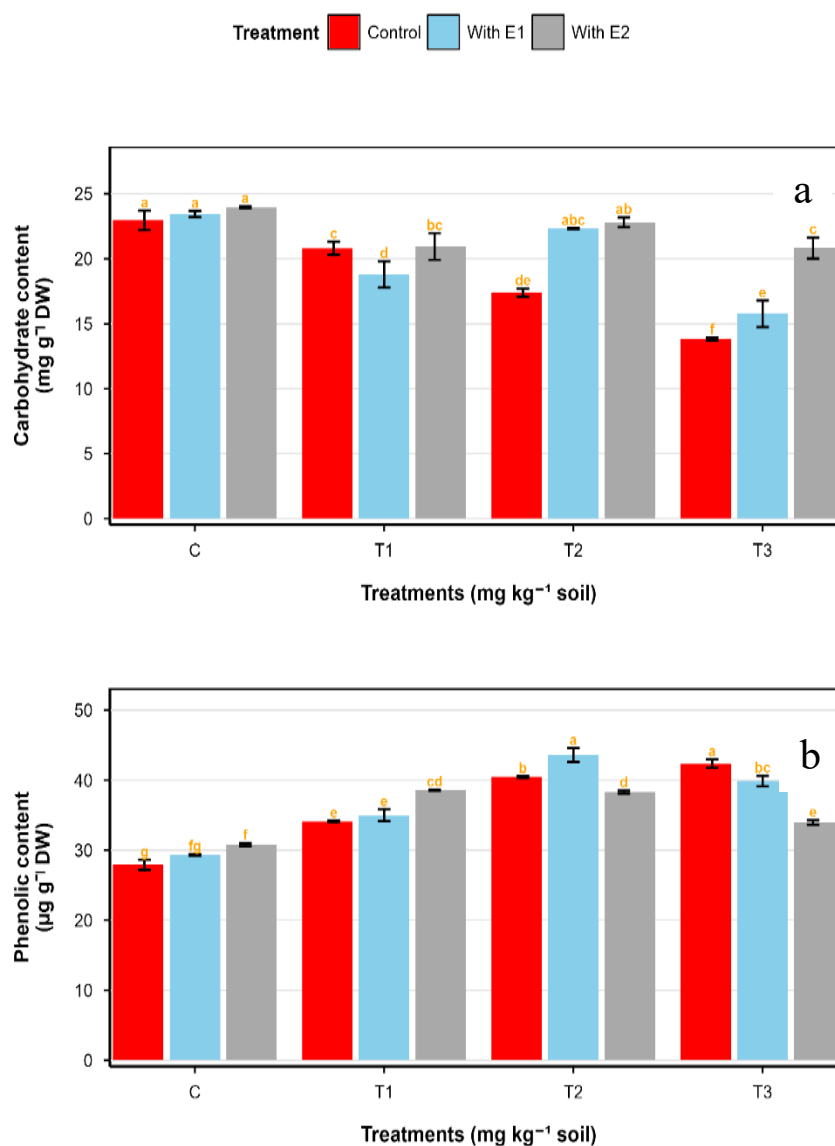


Figure 7: Showing the effect of different concentrations of Cr (50, 100, and 150 μ M) with or without MeJA (50, 100 μ M) on plant biochemical attributes. a) effect on Carbohydrate content, b) effect on Total phenolic content. Data are presented as mean $\pm$ SD (n = 3). Significant differences among treatments were determined by one-way ANOVA followed by Tukey's HSD test ($P \leq 0.05$), indicated by different letters (a-f).

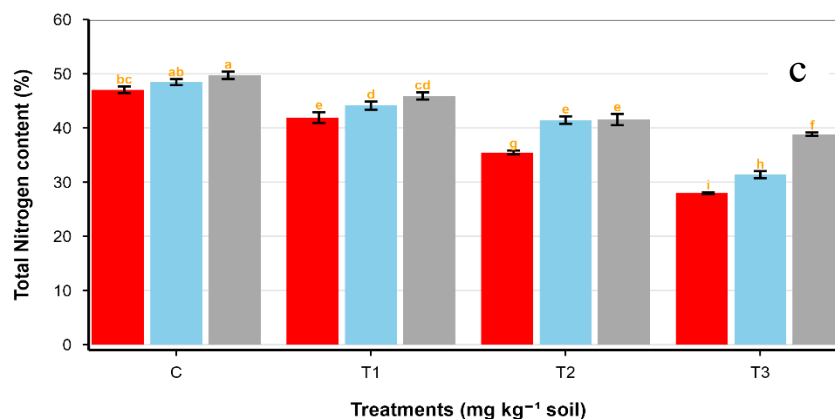
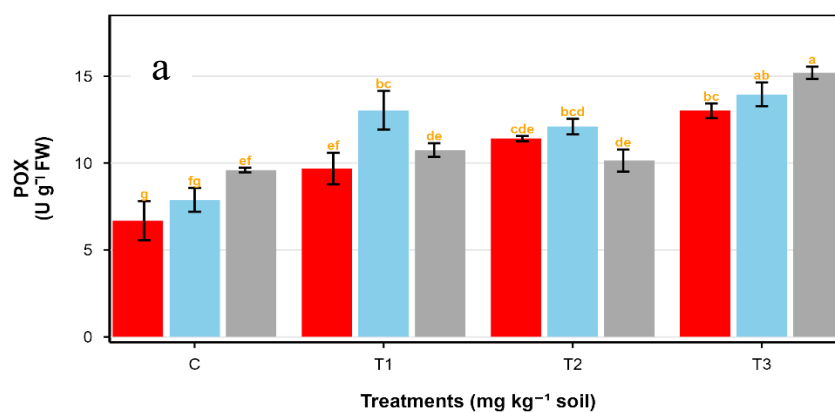


Figure 7c: Showing the effect of different concentrations of Cr (50, 100, and 150 μM) with or without MeJA (50, 100 μM) on Total Nitrogen content. Data are presented as mean $\pm$ SD ($n = 3$). Significant differences among treatments were determined by one-way ANOVA followed by Tukey's HSD test ($P \leq 0.05$), indicated by different letters (a-f).

Effect on Antioxidant Enzyme Activity

Chromium (Cr) stress significantly increased the concentration-dependent activities of three important antioxidant enzymes: peroxidase (POD), catalase (CAT), and superoxide dismutase (SOD). These effects were further amplified by the co-application of methyl jasmonate (MeJA). MeJA supplementation further increased SOD to 11.30–15.30 U mg^{-1} protein, with the highest increase (+82.9%) seen at 150 μM Cr + 50 μM MeJA. SOD activity increased from 8.36 U mg^{-1} protein in the control to 11.02, 11.31, and 14.22 U mg^{-1} protein at 50, 100, and 150 μM Cr, respectively, as shown in (Fig. 8a). Similarly, under Cr stress, CAT activity increased from 0.276 U mg^{-1} protein in control plants to 0.332–0.411 U mg^{-1} protein. Co-application of MeJA increased it even more to 0.532 U mg^{-1} protein at 150 μM Cr + 100 μM MeJA (+93% vs. control) as shown in (Fig. 8b). The same pattern was seen in POD activity, which rose from 6.68 U mg^{-1} protein in controls to 9.73–13.44 U mg^{-1} protein under Cr stress and to 15.19 U mg^{-1} protein (+127%) with MeJA supplementation at 150 μM Cr + 100 μM MeJA as shown in (Fig. 8c). These results show that MeJA synergistically strengthens this protective response, especially at higher Cr concentrations, and that Cr causes oxidative stress in a dose-dependent manner, inducing enzymatic antioxidant defense.



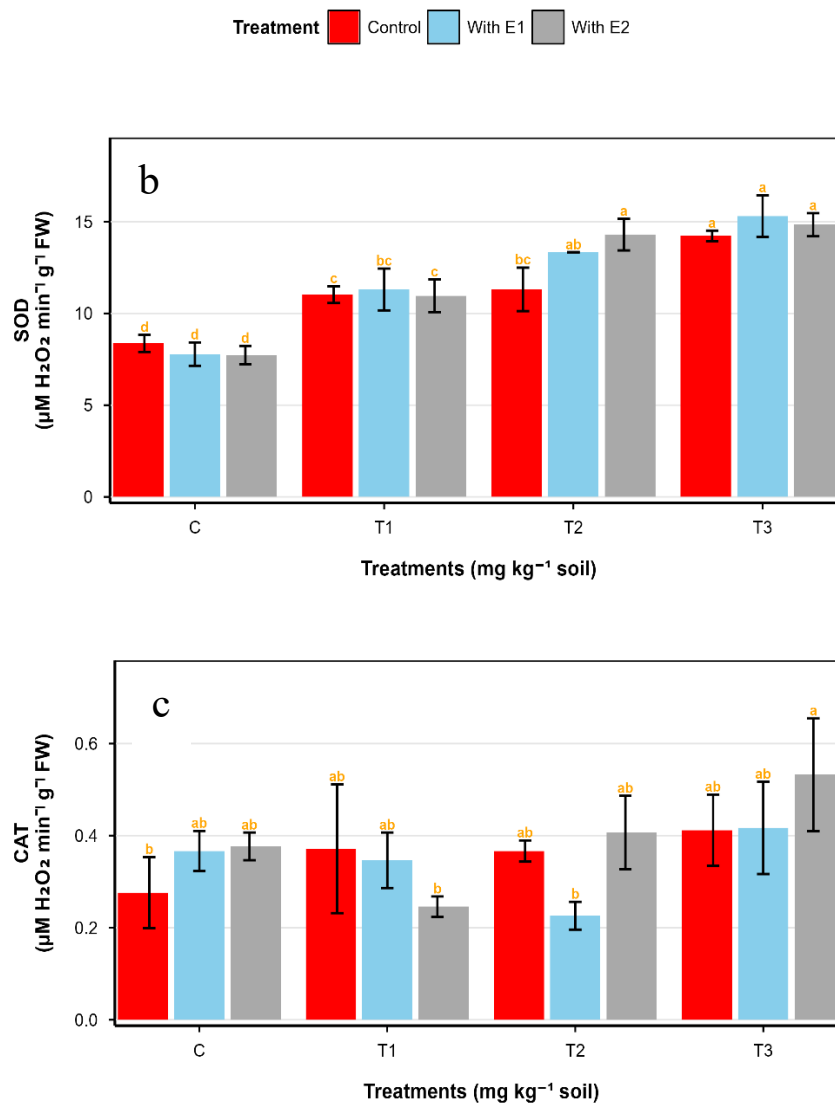


Figure 8: Showing the effect of different concentrations of Cr (50, 100, and 150 μM) with or without MeJA (50, 100 μM) on plant antioxidant enzyme activity. a) effect on POD activity, b) effect on SOD activity. c) effect on CAT activity. Data are presented as mean $\pm$ SD ($n = 3$). Significant differences among treatments were determined by one-way ANOVA followed by Tukey's HSD test ($P \leq 0.05$), indicated by different letters (a-f).

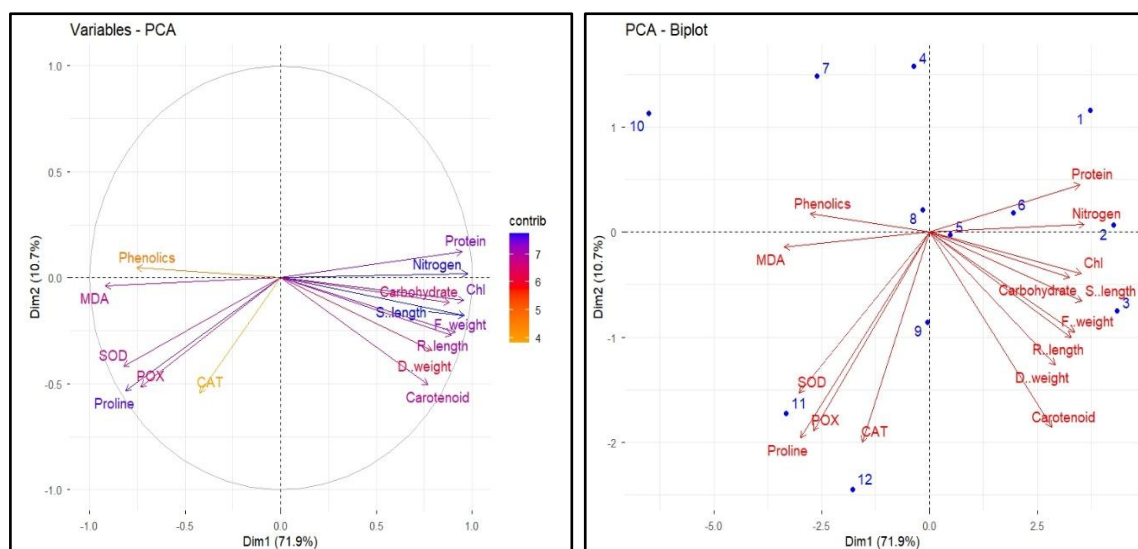


Figure 9: Principal Component Analysis (PCA) plot of variables shows how each biochemical parameter correlates with the first two dimensions. The color gradient shows how much (%) each variable contributes toward the principal components, with purple indicating a higher contribution and yellow a lower. Protein, as well as carbohydrate, with total photosynthetic pigments content and plant height, contribute the most to Dim1. Antioxidant enzymes such as SOD, CAT, and POD, with MDA and Phenolics and Proline content, notably contribute to Dim2. The plot gives insight into how parameters influence the variation across experimental conditions. (b) Principal Component Analysis (PCA) biplot shows the distribution of experimental treatments with (blue numbers) since the first two principal components have dimensions that are (Dim1 = 71.9%, Dim2 = 10.7%). Red arrows represent biochemical variables and their direction. The arrows also show influence magnitude. The angle of the arrows reflects the correlation between the variables, and longer arrows indicate a stronger contribution to the principal components.

Pearson Correlation Heatmap

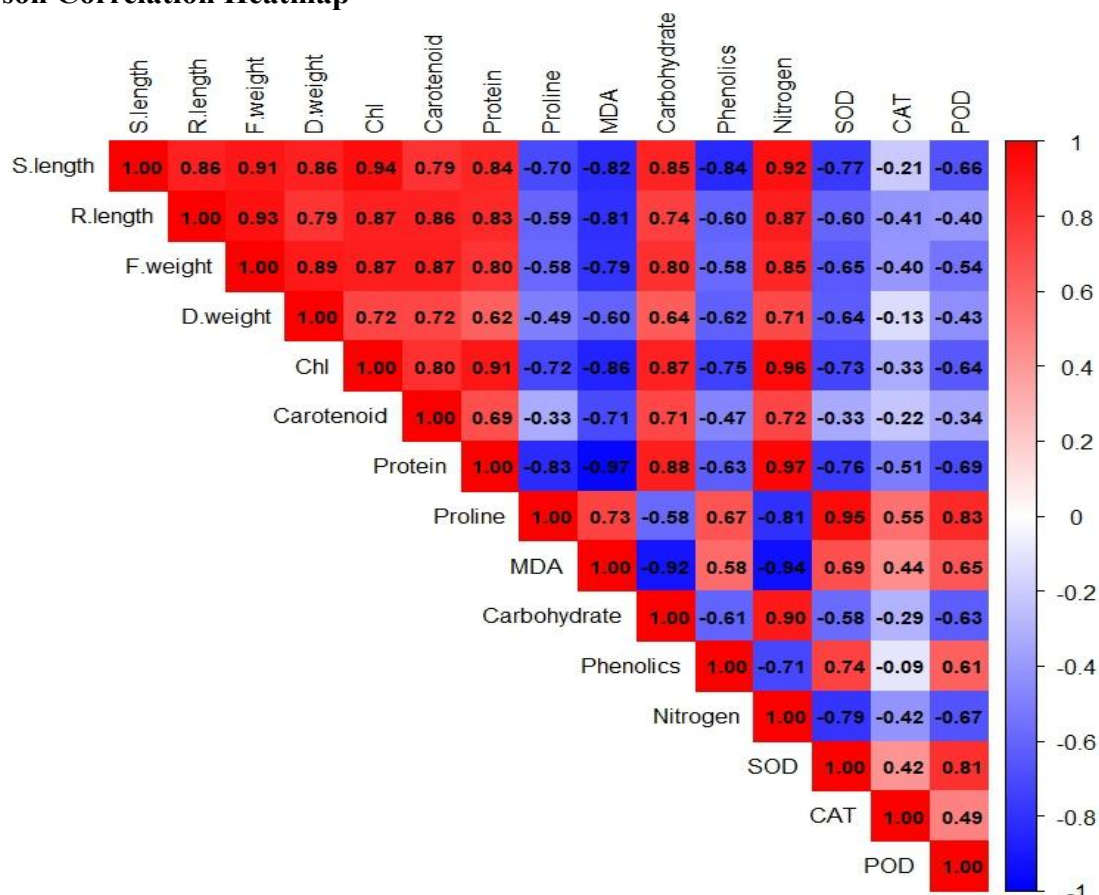


Figure 9c. Correlation matrix of 15 measured parameters for tomato seedlings under 3 treatment combinations under Cr stress conditions based on Pearson's correlation matrix. Shoot length, Root length, Plant Fresh weight, Dry weight, Chlorophyll, Carotenoid content, Protein content, Proline accumulation, MDA content, Carbohydrates, Phenolics, Nitrogen content, SOD, CAT, and POD activities.

Discussion

Due to industries' uncontrolled release of hazardous effluents containing chromium into the environment, chromium toxicity has impacted agricultural soil all over the world. Cr is one HM pollutant that negatively affects plants. During seed germination, heavy metals, particularly Cr, alter a number of physiological functions and biochemical pathways, which may lead to an increase or decrease in the synthesis of different metabolites. These results concur with those of Kundu et al. (2018). This study examines how plant growth and antioxidant enzyme activities are affected by chromium (Cr) stress and assesses the potential benefits of applying exogenous methyl jasmonate (MeJA). In a dose-dependent manner, Cr stress markedly reduced the growth of both shoots and roots, with the most noticeable decreases occurring at 150 μM Cr. MeJA supplementation, however, significantly reduced these growth impairments, particularly at 100 μM concentration, underscoring its function in boosting plant resistance to HM stress.

Reactive oxygen species (ROS) are produced as a result of the well-known Cr-induced oxidative stress phenomenon, and these ROS damage proteins, lipids, nucleic acids, and other components of cells. This oxidative damage has a detrimental effect on the growth and development of plants. Rehman et al. (2023) found that

Brassica parachinensis exhibited significant reductions in root and shoot lengths under Cr exposure, which is in line with the observed decrease in shoot and root lengths under Cr stress. Similar observations regarding *Basella alba* L. have been made by other researchers (Zewail et al., 2020). The accumulation of Cr in roots, which harms the shoot ultrastructure, may be the cause of the shorter root lengths under Cr toxicity in the current study. Furthermore, it has been shown that Cr treatments shorten the roots' and shoots' lengths and lower the fresh and dry weights of a variety of plant species, including *O. sativa* (Ma et al., 2016). However, MJ supplementation (50 and 100 μ M) enhanced plant biomass and growth while mitigating the negative effects of Cr toxicity. Better nutrient and water uptake, cellular redox homeostasis maintenance, enhanced carbon metabolism, and a more robust antioxidant defense system may result from exogenous MJ application that increases plant growth and biomass in Cr-stressed plants. It has been demonstrated that heavy metal toxicity impairs the function of the photosynthetic machinery and thereby reduces plant growth by damaging the thylakoid membrane and photosynthetic pigments (Ghorbani et al. 2021). The findings demonstrated that Cr stress decreased photosynthetic pigments, which may be because of increased activity of the enzyme chlorophyllase, which breaks down chlorophyll, and damage to chloroplasts and chlorophyll-protein complexes from harmful radicals. Earlier report also showed this (Ahmad et al. 2020; Kamran et al. 2021). Cr reduces the amount of chlorophyll by inhibiting enzymes that are necessary for the biosynthesis of chlorophyll (Handa et al. 2019; Ulhassan et al. 2019). This suggests that the toxicity of Cr lowers the absorption of iron and magnesium, which are necessary for chlorophyll biosynthesis, thus lowering chlorophyll synthesis. However, in plants exposed to Cr, MJ improved the function of the photosynthetic machinery and restored levels of carotenoids and chlorophyll, suggesting that MJ protects the photosynthetic machinery from Cr toxicity. Increased activity of enzymes linked to the Calvin cycle and increased uptake of essential nutrients (especially Fe, Ca, K, Mn, and Mg) in biochemical processes involved in chlorophyll biosynthesis may be the cause of MJ's stimulatory effects on photosynthetic pigments and the photosynthetic machinery under Cr toxicity (Mostofa et al. 2015; Mir et al. 2018). Under chromium (Cr) stress, protein content dramatically dropped. As Cr concentrations increased, protein levels in our study decreased gradually, moving from mild stress at 50 mM Cr (-27.20%) to severe stress at 150 mM Cr (-46.85%). This pattern is consistent with previous studies showing that proteins and photosynthetic pigments are oxidatively damaged by reactive oxygen species (ROS) generated by Cr toxicity (Sharma et al., 2020; Srivastava et al., 2021). However, concurrent application of methyl jasmonate (MeJA) reduced these side effects. For example, 100 μ M MeJA with 150 μ M Cr reduced Cr-induced protein loss to -29.79%, while 50 μ M MeJA slightly raised protein content in the controlled plant (+7.86%). MeJA is known to activate antioxidant enzymes and stress-responsive pathways to scavenge ROS, stabilize cellular proteins, and maintain photosynthetic efficiency under metal stress (Iftikhar et al., 2025; Pu et al., 2025). MeJA's protective effect raises the possibility that it could improve plants' metabolic resilience to Cr stress. Despite heavy metal toxicity, MeJA promotes protein synthesis and photosynthetic pigment levels by increasing antioxidant activity and upregulating genes associated with stress (Sharma et al., 2020; Iftikhar et al., 2025). Overall, the results support the use of MeJA as a protective agent in plants exposed to heavy metal stress by showing that, despite the fact that exposure to Cr significantly reduces protein content, its application, especially at higher concentrations (100 μ M), effectively mitigates these effects (Srivastava et al., 2021; Pu et al., 2025).

Proline's protective function differs depending on the species. Proline production and accumulation in the plant increased quickly as the Cr concentration rose to 150 μ M. This result was anticipated since proline is regarded as

an energy source. Its oxidative metabolism in the mitochondria promotes oxidative phosphorylation and ATP synthesis in healing tissues. Karthik et al. (2016) reported similar findings of elevated proline levels caused by Cr toxicity in *P. vulgaris*. Our results showed that MDA content increased significantly as Cr levels increased. The oxidative damage brought on by Cr toxicity may be connected to the rise in ROS. It is well known that Cr stress results in lipid peroxidation and an excess of ROS (superoxide and H₂O₂). However, proteins, lipids, and DNA are among the vital cell macromolecules that are harmed by ROS at higher concentrations. ROS functions as a chemical messenger at low concentrations that controls plant responses by means of hormones (Pourrut et al., 2013). By interfering with the mitochondrial respiratory chain, ROS-induced lipid peroxidation weakens biological membranes and makes them susceptible to oxidative damage. Therefore, it is believed that lipid peroxidation is a sign of oxidative stress in plants. MDA is also used as an indicator of oxidative stress because it is a notable byproduct of lipid peroxidation. However, the application of MJ had a protective effect by significantly reducing the production of MDA content. Additionally, the findings demonstrated that Cr toxicity reduced total carbohydrate levels, which may be a sign of reduced carbon absorption and damage to the photosynthetic machinery. Consequently, reducing the internal level of carbon resources because of Cr toxicity may hinder growth by reducing ATP, NADP, and other compounds needed for plant metabolic processes. (Osyczka et al. 2021). The effects of chromium (Cr) stress were reversed by methyl jasmonate (MeJA), which significantly reduced the buildup of carbohydrates in plants. Under control, the average amount of carbohydrates was 22.95 units; during MeJA treatment, this amount increased slightly (2.15–4.36%). Fatma et al. (2021) also suggested that MJ increased the amount of carbohydrates, in accordance with a prior study by Kamran et al. (2021). Cr exposure at 50, 100, and 150 μ M caused declines of 9.32%, 24.20%, and 39.74%, respectively (Qin et al., 2024; Zhu et al., 2024). These losses were lessened by MeJA supplementation, which reduced declines to as low as 9.24% under 150 μ M Cr and 0.67% under 100 mM Cr (Pu et al., 2025; Wu et al., 2024). MeJA might be a helpful strategy to sustain carbohydrate metabolism under Cr stress (Khan et al., 2025; Yu et al., 2024). The maintenance of cellular homeostasis, the enhancement of antioxidant enzymes, and the activation of stress-responsive genes are probably all involved in this protective effect (Manzoor et al., 2022; Aslam et al., 2021). One important defense mechanism against oxidative stress caused by heavy metals (HMs) such as chromium (Cr) is the accumulation of total phenolic content (TPC) in plant tissues. As Cr concentrations rose in our investigation, TPC rose as well, suggesting an adaptive reaction to oxidative stress. Nevertheless, TPC dropped at 150 μ M Cr, most likely as a result of the plant's extreme oxidative damage, which prevented it from producing phenolic compounds. This is consistent with research by Anjum et al. (2017), which found that Cr toxicity increased levels of free proline, soluble sugars, and total phenolics while decreasing levels of soluble protein. Their findings point to a complex interrelationship between metabolic pathways and stress responses. TPC levels in our study were markedly elevated by the administration of methyl jasmonate (MeJA), a plant hormone known to regulate stress responses. This is in line with research by Ho et al. (2020), which showed that MeJA treatment raised *P. multiflorum*'s phenolic content, indicating its function in triggering the production of secondary metabolites under stress. The progressive decrease in nitrogen content observed in our study as Cr concentrations increased indicates that plants' capacity to assimilate nitrogen is significantly hampered by chromium (Cr) stress. This decrease in nitrogen levels under Cr exposure is in line with a study by Qin et al. (2024) that found that plants' nitrogen metabolism is negatively impacted by Cr stress. Higher concentrations of methyl jasmonate (MeJA) offered greater protection, and its application lessened the detrimental effect of Cr on nitrogen content. This is consistent with the findings of Nazir et al. (2023), who

found that MeJA pretreatment increased the activities of glutamine synthetase and nitrate reductase, which facilitated the assimilation of nitrogen during drought stress. Antioxidant enzyme activity rose in tandem with the amount of Cr in *A. sativa* L. leaves. By encouraging the antioxidant activities of SOD, POD, and CAT, plants defend themselves against oxidative damage brought on by Cr stress. The antioxidant enzyme activities in the current study varied in tandem with the Cr concentration. Reactive oxygen species (ROS), which can oxidatively damage plant cells, are known to be produced by exposure to Cr. Sharma and Dietz (2009) found that antioxidant enzymes are activated in response to Cr-induced oxidative stress to decrease, which is consistent with the fact that SOD activity increased significantly from 8.36 U mg⁻¹ protein in control plants to 14.22 U mg⁻¹ protein at 150 mM Cr. Similar to the dose-dependent increase in CAT and POD activity observed in this study, Gupta and Huang (2014) discovered that Cr exposure raises these enzymes' activities as part of the plant's defense mechanism against oxidative stress. The results of this investigation shed important light on the processes through which plant physiology is impacted by Cr stress and how MeJA can lessen these impacts. MeJA's synergistic effect and the dose-dependent increase in antioxidant enzyme activities under Cr stress suggest that it could be a useful tool for enhancing plant resistance to Cr-induced oxidative stress as shown in **Figure 10**. This has real-world ramifications for farming methods, especially in regions where heavy metal contamination of the soil exists.

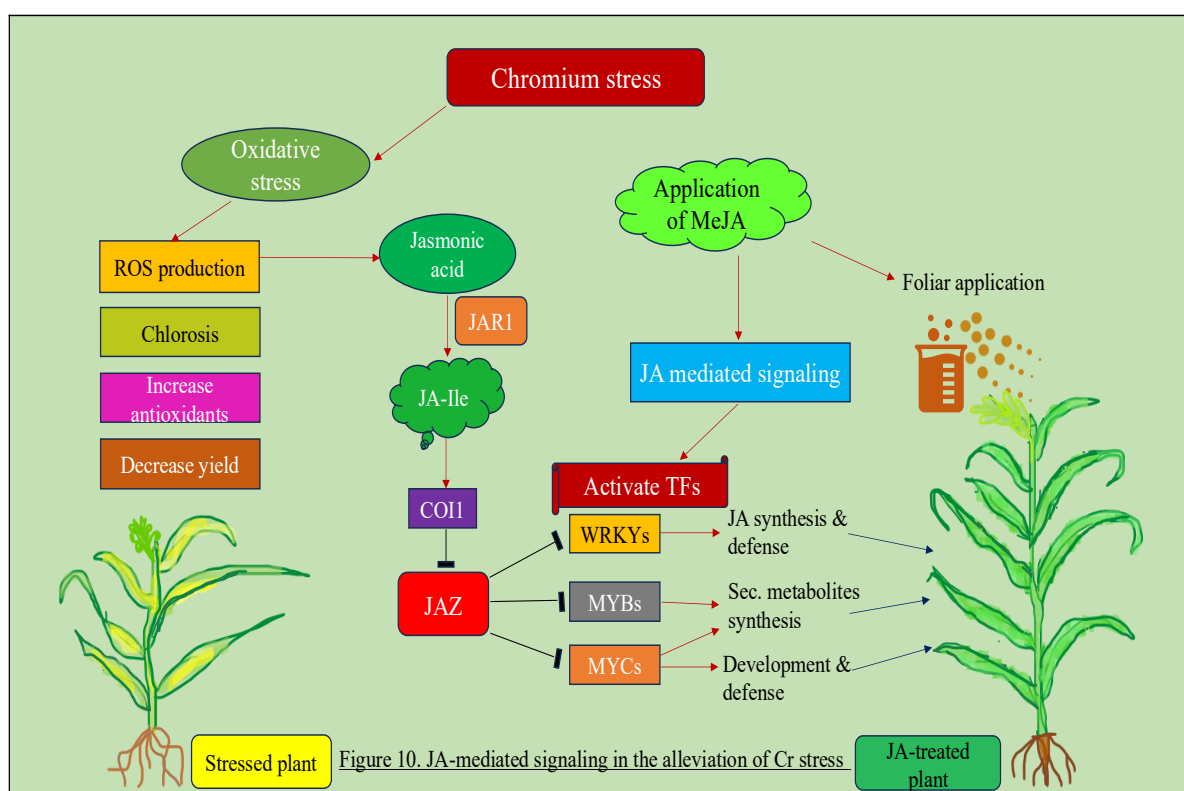


Figure 10. Diagrammatic representation of the Cr effect on the plant and the alleviating effect of exogenous application of Methyl jasmonate.

Conclusion

In this study we concluded that, by disrupting essential physiological and biochemical functions, chromium (Cr) stress significantly impairs plant growth and development. It significantly lowers nitrogen uptake, protein and carbohydrate content, photosynthetic pigments, shoot and root growth, and oxidative stress brought on by an excess of reactive oxygen species (ROS). Increased levels of malondialdehyde (MDA), a lipid peroxidation indicator brought on by this oxidative stress, are indicative of severe cellular membrane damage and compromised metabolic processes. Proline, phenolics, and antioxidant enzymes like SOD, POD, and CAT are some of the ways that plants react to Cr toxicity. These protective mechanisms, however, are typically insufficient at high Cr concentrations, resulting in significant oxidative damage. These negative effects are significantly lessened by exogenous application of methyl jasmonate (MeJA), which increases antioxidant enzyme activity, decreases MDA accumulation, stabilizes proteins and photosynthetic machinery, and maintains metabolic and cellular homeostasis. MeJA supports the accumulation of carbohydrates and secondary metabolites, promotes nutrient uptake, and fortifies the plant's defense mechanism. MeJA's potent antioxidant-stimulating and membrane-protective qualities show that it could be a practical tactic to boost plant resilience and productivity in heavy metal-contaminated environments.

Future Perspectives

This study highlights methyl jasmonate (MeJA) as a potentially effective approach for mitigating chromium (Cr) stress in plants. Future research should focus on elucidating the molecular mechanisms underlying MeJA-mediated enhancement of antioxidant defense, including detailed investigations of metal transporter gene expression. In addition, the interactive effects of MeJA with other plant growth regulators and beneficial microorganisms, as well as its effectiveness across different crop species and field conditions, warrant comprehensive evaluation. Under heavy metal-contaminated environments, the integration of MeJA application with soil remediation strategies may further improve plant resilience, enhance productivity, and reduce the entry of toxic metals into the food chain.

Acknowledgment

The authors sincerely thank the CSIR- (UGC) University Grant Commission for financial support. Additionally, we acknowledge the Department of Botany, Chaudhary Charan Singh University, Meerut (U.P.) India.

Author information

Authors and affiliation

Phytochemistry & Metabolic Studies Laboratory, Department of Botany, Chaudhary Charan Singh University, Meerut, Uttar Pradesh-250001, India.

Salim Salim, Shivani Chauhan, Rajesh Pareek, and Ishwar Singh

Contributions

Conceptualized the literature work's design, draft, and layout - Salim Salim, Shivani Chauhan, Rajesh Pareek.

Preparation of the figures - Salim Salim and Shivani Chauhan

Editing the manuscript – Ishwar Singh

All the authors have critically reviewed the manuscript and approved it for submission.

Corresponding author

Correspondence to Ishwar Singh

Ethics declarations**Ethical approval**

This is not applicable

Informed consent

This is not applicable

Conflict of interest

The authors declare that they have no conflict of interest.

Data availability

The Corresponding author will provide all data files supporting the findings of this study.

References

- Aebi, H. (1984). Methods in Enzymology.
- Ahmad, R., Ali, S., Abid, M., Rizwan, M., Ali, B., Tanveer, A., ... & Ghani, M. A. (2020). Glycine betaine alleviates the chromium toxicity in *Brassica oleracea* L. by suppressing oxidative stress and modulating the plant morphology and photosynthetic attributes. *Environmental Science and Pollution Research*, 27, 1101-1111.
- Ahmad, R., Ali, S., Rizwan, M., Dawood, M., Farid, M., Hussain, A., ... & Ahmad, P. (2020). Hydrogen sulfide alleviates chromium stress on cauliflower by restricting its uptake and enhancing the antioxidative system. *Physiologia plantarum*, 168(2), 289-300.
- Alam, M. M., Nahar, K., Hasanuzzaman, M., & Fujita, M. (2014). Exogenous jasmonic acid modulates the physiology, antioxidant defense, and glyoxalase systems in imparting drought stress tolerance in different *Brassica* species. *Plant Biotechnology Reports*, 8, 279-293.
- Ali, S., Khan, N., & Rehman, M. (2024). Toxic metal contamination in soil and food chains: Emerging risks and management strategies. *Environmental Pollution*, 343, 123091. <https://doi.org/10.1016/j.envpol.2024.123091>
- Anjum, S. A., Ashraf, U., Khan, I., Tanveer, M., Shahid, M., Shakoor, A., & Wang, L. C. (2017). Phyto-toxicity of chromium in maize: Oxidative damage, osmolyte accumulation, antioxidant defense, and chromium uptake. *Pedosphere*, 27(2), 262-273.
- Ao, M., Chen, X., Deng, T., Sun, S., Tang, Y., Morel, J. L., et al. (2022). Chromium biogeochemical behaviour in soil-plant systems and remediation strategies: A critical review. *J. Hazard Mat.* 424, 127233. doi: 10.1016/j.jhazmat.2021.127233
- Azeez, N. A., Dash, S. S., Gummadi, S. N., Deepa, V. S. (2021). Nano-remediation of toxic heavy metal contamination: Hexavalent chromium [Cr(VI)]. *Chemosphere* 266, 129204. doi: 10.1016/j.chemosphere.2020.129204
- Bates, L. S., Waldren, R. P. A., & Teare, I. D. (1973). Rapid determination of free proline for water-stress studies. *Plant and soil*, 39, 205-207.
- Dampare, S. B., Ameyaw, Y., Adotey, D. K., Osae, S., Serfor-Armah, Y., Nyarko, B. J. B., & Adomako, D. (2006). Seasonal trend of potentially toxic trace elements in soils supporting medicinal plants in the eastern region of Ghana. *Water, Air, and Soil Pollution*, 169, 185-206.
- Daud, M. K., Ali, S., Variath, M. T., Khan, M., Jamil, M., Ahmad, M., & Zhu, S. J. (2021). Chromium (VI)-induced leaf-based differential physiological, metabolic and microstructural changes in two transgenic cotton cultivars (J208, Z905) and their hybrid line (ZD14). *Journal of Plant Growth Regulation*, 1-13.
- Dheeba, B., Sampathkumar, P., & Kannan, K. (2015). Fertilizers and mixed crop cultivation of chromium-tolerant and sensitive plants under chromium toxicity. *Journal of Toxicology*, 2015(1), 367217.

- Diwan, H., Khan, I., Ahmad, A., & Iqbal, M. (2010). Induction of phytochelatins and antioxidant defence system in *Brassica juncea* and *Vigna radiata* in response to chromium treatments. *Plant Growth Regulation*, 61, 97-107.
- FAO. (2024). *FAOSTAT statistical database: Crops and livestock products*. Food and Agriculture Organization of the United Nations.
- Farhangi-Abriz, S., & Ghassemi-Golezani, K. (2018). How can salicylic acid and jasmonic acid mitigate salt toxicity in soybean plants. *Ecotoxicology and environmental safety*, 147, 1010-1016.
- Fatma, M., Khan, M. I. R., & Khan, N. A. (2021). Methyl jasmonate protects the PS II system by maintaining the stability of chloroplast D1 protein and accelerating enzymatic antioxidants in heat-stressed wheat plants. *Antioxidants*, 10(8), 1216.
- Ghorbani, A., Pishkar, L., Roodbari, N., Pehlivan, N., & Wu, C. (2021). Nitric oxide could allay arsenic phytotoxicity in tomato (*Solanum lycopersicum* L.) by modulating photosynthetic pigments, phytochelatin metabolism, molecular redox status and arsenic sequestration. *Plant Physiology and Biochemistry*, 167, 337-348.
- Ghorbani, A., Pishkar, L., Roodbari, N., Tavakoli, S. A., Jahromi, E. M., & Wu, C. (2023). Nitrate reductase is needed for methyl jasmonate-mediated arsenic toxicity tolerance of rice by modulating the antioxidant defense system, glyoxalase system and arsenic sequestration mechanism. *Journal of Plant Growth Regulation*, 42(2), 1107-1119.
- Ghosh, U. C., Dasgupta, M., Debnath, S., & Bhat, S. C. (2003). Studies on management of chromium (VI)–contaminated industrial waste effluent using hydrous titanium oxide (HTO). *Water, Air, and Soil Pollution*, 143, 245-256.
- Gupta, D. K., & Huang, H. (2014). Chromium toxicity and tolerance in plants. *Environmental Chemistry Letters*, 12(4), 383–400.
- Gupta, R., Sharma, P., & Singh, A. (2024). Mining-induced heavy metal pollution: Global health implications and mitigation approaches. *Science of the Total Environment*, 922, 171684. <https://doi.org/10.1016/j.scitotenv.2024.171684>
- Handa, N., Kohli, S. K., Sharma, A., Thukral, A. K., Bhardwaj, R., Abd_Allah, E. F., ... & Ahmad, P. (2019). Selenium modulates dynamics of antioxidative defence expression, photosynthetic attributes and secondary metabolites to mitigate chromium toxicity in *Brassica juncea* L. plants. *Environmental and Experimental Botany*, 161, 180-192.
- Heath, R. L., & Packer, L. (1968). Photoperoxidation in isolated chloroplasts: I. Kinetics and stoichiometry of fatty acid peroxidation. *Archives of biochemistry and biophysics*, 125(1), 189-198.
- Ho, T.-T., Murthy, H. N., & Park, S.-Y. (2020). Methyl jasmonate induced oxidative stress and accumulation of secondary metabolites in plant cell and organ cultures. *International Journal of Molecular Sciences*, 21(3), 716.
- Hussain, A., Ali, S., Rizwan, M., ur Rehman, M. Z., Javed, M. R., Imran, M., ... & Nazir, R. (2018). Zinc oxide nanoparticles alter the wheat physiological response and reduce the cadmium uptake by plants. *Environmental Pollution*, 242, 1518-1526.
- ICAR-Indian Grassland and Fodder Research Institute (IGFRI). (2015). *Vision 2050*. Jhansi, India: ICAR-IGFRI. Retrieved from <https://www.igfri.res.in/>
- Iftikhar, F., Zulfiqar, A., Kamran, A. *et al.* (2025) Antioxidant Responses in Chromium-Stressed Maize as Influenced by Foliar and Root Applications of Fulvic Acid. *Sci Rep* 15, 1289. <https://doi.org/10.1038/s41598-024-84803-4>
- IndexBox. (2024). *World - Oats - Market analysis, forecast, size, trends and insights*. Retrieved from Indian Council of Agricultural Research (ICAR). (2023–2024). *SeedNet India Portal – Breeder and certified seed production data*. Department of Agriculture and Farmers Welfare, Government of India.

- Kamran, M., Khan, M. I. R., & Ahmad, P. (2021). Jasmonic acid-mediated enhanced regulation of oxidative stress and growth under chromium stress. *Environmental and Experimental Botany*, 187, 104488.
- Kamran, M., Wang, D., Alhaithloul, H. A. S., Alghanem, S. M., Aftab, T., Xie, K., ... & Soliman, M. H. (2021). Jasmonic acid-mediated enhanced regulation of oxidative, glyoxalase defense system and reduced chromium uptake contributes to alleviation of chromium (VI) toxicity in choysum (*Brassica parachinensis* L.). *Ecotoxicology and Environmental Safety*, 208, 111758.
- Karimi, N., & Ghasempour, H. R. (2019). Salicylic acid and jasmonic acid restrains nickel toxicity by ameliorating antioxidant defense system in shoots of metallicolous and non-metallicolous *Alyssum inflatum* Náy. Populations. *Plant Physiology and Biochemistry*, 135, 450-459.
- Karthik, C., Oves, M., Thangabalu, R., Sharma, R., Santhosh, S. B., & Arulselvi, P. I. (2016). Cellulosimicrobium funkei-like enhances the growth of *Phaseolus vulgaris* by modulating oxidative damage under Chromium (VI) toxicity. *Journal of advanced research*, 7(6), 839-850.
- Kundu, D., Dey, S., & Raychaudhuri, S. S. (2018). Chromium (VI)–induced stress response in the plant *Plantago ovata* Forsk in vitro. *Genes and Environment*, 40(1), 21.
- Ma, J., Lv, C., Xu, M., Chen, G., Lv, C., & Gao, Z. (2016). Photosynthesis performance, antioxidant enzymes, and ultrastructural analyses of rice seedlings under chromium stress. *Environmental Science and Pollution Research*, 23(2), 1768-1778.
- Maehly, A. C. (1954). The assay of catalases and peroxidases. *Methods of biochemical analysis*, 357-424.
- Mir, M. A., John, R., Alyemeni, M. N., Alam, P., & Ahmad, P. (2018). Jasmonic acid ameliorates alkaline stress by improving growth performance, ascorbate glutathione cycle and glyoxylase system in maize seedlings. *Scientific Reports*, 8(1), 2831.
- Mostofa, M. G., Rahman, A., Ansary, M. M. U., Watanabe, A., Fujita, M., & Tran, L. S. P. (2015). Hydrogen sulfide modulates cadmium-induced physiological and biochemical responses to alleviate cadmium toxicity in rice. *Scientific reports*, 5(1), 14078.
- Mousavi, S. R., Niknejad, Y., Fallah, H., & Tari, D. B. (2020). Methyl jasmonate alleviates arsenic toxicity in rice. *Plant cell reports*, 39(8), 1041-1060.
- Nakano, Y., & Asada, K. (1981). Hydrogen peroxide is scavenged by ascorbate-specific peroxidase in spinach chloroplasts. *Plant and cell physiology*, 22(5), 867-880.
- Nazir, F., Shah, A. N., Khan, M. I., & Shahid, M. (2023). Methyl jasmonate pretreatment promotes nitrogen assimilation under drought stress. *Environmental and Experimental Botany*, 202, 104992.
- Osyczka, P., Latkowska, E., & Rola, K. (2021). Metabolic processes involved with sugar alcohol and secondary metabolite production in the hyperaccumulator lichen *Diploschistes muscorum* reveal its complex adaptation strategy against heavy-metal stress. *Fungal biology*, 125(12), 999-1008.
- Pourrut, B., Shahid, M., Douay, F., Dumat, C., & Pinelli, E. (2013). Heavy metal stress in plants. *Molecular Mechanisms Involved in Lead Uptake, Toxicity and Detoxification in Higher Plants*, 121-147.
- Pu, K., Li, N., Gao, Y., Wang, T., Zhang, M., Sun, W., Li, J., & Xie, J. (2025). Mitigating effects of Methyl Jasmonate on photosynthetic inhibition and oxidative stress of pepper (*Capsicum annuum* L) seedlings under low temperature combined with low light. *Plant physiology and biochemistry: PPB*, 223, 109843.
- Pu, K., Liu, Y., Zhang, X., & Wang, C. (2025). Mitigating effects of methyl jasmonate on photosynthetic performance and antioxidant capacity under abiotic stress. *Journal of Plant Physiology*, 285, 153–162.
- Pushkar, B., Sevak, P., Parab, S., Nilkanth, N. (2021). Chromium pollution and its bioremediation mechanisms in bacteria: A review. *J. Environ. Manage.* 287, 112279. doi: 10.1016/j.jenvman.2021.112279
- Qin, C., Zhang, Y., & Li, X. (2024). Chromium-mediated damaging effects on growth, nitrogen metabolism, and antioxidant defense in plants. *Environmental and Experimental Botany*, 202, 104993.

- Rehman, M., Saeed, M. S., Fan, X., Salam, A., Munir, R., Yasin, M. U., Khan, A. R., Muhammad, S., Ali, B., Ali, I., Khan, J., & Gan, Y. (2023). The multifaceted role of jasmonic acid in plant stress mitigation: An overview. *Plants*, 12(23), 3982.
- Sharma, A., Kapoor, D., Wang, J., Shahzad, B., Kumar, V., Bali, A. S., Jasrotia, S., Zheng, B., Yuan, H., & Yan, D. (2020). Chromium Bioaccumulation and Its Impacts on Plants: An Overview. *Plants (Basel, Switzerland)*, 9(1), 100.
- Sharma, P., & Dietz, K. J. (2009). The relationship between metal toxicity and cellular redox imbalance. *Trends in Plant Science*, 14(1), 43–50.
- Singh, D., Sharma, N. L., Singh, C. K., Sarkar, S. K., Singh, I., & Dotaniya, M. L. (2020). Effect of chromium (VI) toxicity on morpho-physiological characteristics, yield, and yield components of two chickpea (*Cicer arietinum* L.) varieties. *PloS one*, 15(12), e0243032. <https://doi.org/10.1371/journal.pone.0243032>
- Singh, H. P., Mahajan, P., Kaur, S., Batish, D. R., & Kohli, R. K. (2013). Chromium toxicity and tolerance in plants. *Environmental Chemistry Letters*, 11, 229-254.
- Srivastava, D., Tiwari, M., Dutta, P., Singh, P., Chawda, K., Kumari, M., et al. (2021). Chromium stress in plants: Toxicity, tolerance, and phytoremediation. *Sustainability* 13, 4629. doi: 10.3390/su13094629
- Szopińska, M., Dębska, B., & Rutkowska, A. (2019). Effect of hexavalent chromium on oat germination and seedling growth. *Environmental Science and Pollution Research*, 26, 2244–2254.
- The Economic Times. (2023). *India's growing interest in oats for nutrition and health*. The Times Group.
- Ulhasan, Z., Gill, R. A., Huang, H., Ali, S., Mwamba, T. M., Ali, B., ... & Zhou, W. (2019). Selenium mitigates the chromium toxicity in *Brassica napus* L. by ameliorating nutrients uptake, amino acids metabolism and antioxidant defense system. *Plant Physiology and Biochemistry*, 145, 142-152.
- USDA Foreign Agricultural Service. (2023). *Grain: World markets and trade – Oats production estimates*. United States Department of Agriculture. Retrieved from <https://www.fas.usda.gov/data>
- Wang, J., & Chen, C. (2009). Biosorbents for heavy metals removal and their future. *Biotechnology advances*, 27(2), 195-226.
- Wang, J., Li, Y., & Zhou, Q. (2024). Pesticide-associated heavy metal release and combined toxicity in agricultural soils. *Journal of Hazardous Materials*, 471, 134238. <https://doi.org/10.1016/j.jhazmat.2024.134238>
- Wu, J., Li, M., & Chen, L. (2024). Effects of jasmonic acid on stress response and quality improvement in plants. *Molecules*, 29(11), 1557.
- Wyszkowski, M., & Radziemska, M. (2010). Effects of chromium (III) and chromium (VI) on spring barley and oats biomass yield and content of nitrogen compounds. *Journal of Toxicology and Environmental Health Sciences*, 2(5), 73–82.
- Yan, Z., Zhang, W., Chen, J., & Li, X. (2015). Methyl jasmonate alleviates cadmium toxicity in *Solanum nigrum* by regulating metal uptake and antioxidative capacity. *Biologia plantarum*, 59(2), 373-381.
- Zewail, R. M., El-Desoukey, H. S., & Islam, K. R. (2020). Chromium stress alleviation by salicylic acid in Malabar spinach (*Basella alba*). *Journal of Plant Nutrition*, 43(9), 1268-1285.
- Zhao, Y., Hu, C., Wang, X., Qing, X., Wang, P., Zhang, Y., ... & Zhao, X. (2019). Selenium alleviated chromium stress in Chinese cabbage (*Brassica campestris* L. ssp. *Pekinensis*) by regulating root morphology and metal element uptake. *Ecotoxicology and Environmental Safety*, 173, 314-321.