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Synergistic Modulation of Oxidative Defense Pathways in Bitter Gourd under Chromium Toxicity: Integrating Seed Priming Induced Metabolic Reprogramming with Physiological Resilience

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ABSTRACT

Chromium (Cr) contamination poses a persistent threat to agricultural productivity, particularly in regions where industrial discharge continues to percolate into arable soils. Bitter gourd (*Momordica charantia* L.), known for its high therapeutic value, is highly susceptible to Cr-induced oxidative perturbation. In the present study, we investigated how seed priming with soybean and pumpkin seed extracts orchestrates a coordinated biochemical and physiological response that enhances crop resilience under Cr stress. A greenhouse experiment integrating multiple Cr levels with methanolic and aqueous priming treatments revealed that Cr toxicity markedly suppressed shoot elongation, biomass accumulation, water balance, and photosynthetic pigment synthesis while concurrently increasing the levels of reactive oxygen species (ROS), hydrogen peroxide (H_2O_2), and malondialdehyde (MDA). However, primed seeds presented a reprogrammed metabolic landscape characterized by elevated activities of antioxidant enzymes (SOD, CAT, POD),

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enriched pools of phenolics, flavonoids, and ascorbic acid, and improved pigment and water status. Aqueous soybean extract at 1 g L^{-1} emerged as the most potent treatment, nearly restoring photosynthetic integrity and minimizing lipid peroxidation even under high Cr exposure. These findings underscore the synergistic capacity of natural seed extracts to fortify redox buffering systems and stabilize cellular metabolism, offering a sustainable, eco-friendly strategy to mitigate heavy metal toxicity in economically important vegetable crops.

Keywords: Bitter gourd, chromium toxicity, oxidative stress, soybean extract, antioxidant enzymes, stress physiology.

Introduction

Heavy metal contamination has quietly evolved into one of the most insidious threats to global agricultural sustainability, with chromium (Cr) standing out as an especially disruptive pollutant owing to its widespread industrial usage, environmental persistence, and pronounced phytotoxicity (Katz & Salem 1994; Dixit et al. 2002). In regions where tannery effluents, electroplating residues, and pigment-industry wastewaters routinely leach into arable soils, Cr does not merely accumulate but penetrates the physiological architecture of plants, distorting metabolic harmony and suppressing productivity. Once assimilated, Cr interferes with nutrient uptake, inhibits chlorophyll biosynthesis, damages the chloroplast ultrastructure, and accelerates reactive oxygen species (ROS) generation, thereby initiating cascading oxidative injury that manifests as chlorosis, impaired photosynthesis, and severe growth inhibition (Panda & Patra 1997; Shanker et al. 2005; Amin et al. 2013; Wakeel et al. 2020).

Bitter gourd (*Momordica charantia* L.), also known as bitter melon or karela, is a widely cultivated medicinal and vegetable crop belonging to the family Cucurbitaceae. It is valued for its diverse therapeutic and nutritional attributes, including antioxidant, anti-inflammatory, and antidiabetic properties. Bitter, an economically and medicinally important cucurbitaceous vegetable, is highly valued for its abundant bioactive constituents, including phenolics, flavonoids, triterpenoid glycosides, and cucurbitacins, which confer antioxidant, anti-inflammatory, and antidiabetic properties (Grover & Yadav 2004; Behera et al. 2010; Dandawate et al. 2016). However, despite its pharmacological richness, *M. charantia* remains

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vulnerable to abiotic stressors, particularly Cr-driven oxidative disruptions. The heavy metal burden compromises membrane integrity, disturbs osmotic balance, and disrupts essential biochemical pathways, often exceeding the capacity of the intrinsic defense systems of plants (Sharma et al. 2020).

Plants naturally deploy a hierarchical antioxidant network to counteract the accumulation of ROS, including enzymatic components such as catalase (CAT), superoxide dismutase (SOD), and peroxidase (POD), complemented by nonenzymatic antioxidants such as phenolics, flavonoids, and ascorbic acid (Fryzova et al. 2018; Sharma et al. 2020). However, when the intensity of heavy metal stress exceeds a plant's endogenous buffering capacity, this defense machinery becomes insufficient, necessitating external intervention.

Seed priming has emerged as an elegant, low-cost, and environmentally sustainable strategy to precondition seeds before germination, accelerating the activation of metabolic pathways associated with improved vigor, enhanced membrane stability, and heightened stress tolerance (Farooq et al. 2007; Jisha et al. 2013; Rakshit 2015). Through controlled hydration, priming initiates early biochemical activities, increases enzyme activation, promotes nutrient mobilization, and primes stress-responsive signalling cascades, enabling seedlings to respond more rapidly and effectively upon exposure to adverse conditions (Muhammad et al. 2015).

Increasing attention has focused on plant-derived extracts as natural priming agents owing to their rich antioxidant profiles and metal-chelating capabilities. Soybean (*Glycine max*) and pumpkin (*Cucurbita maxima*) seeds are known reservoirs of tocopherols, carotenoids, phenolic acids, flavonoids, and other bioactive metabolites capable of scavenging free radicals, stabilizing cellular membranes, and regulating oxidative stress pathways (Phillips et al. 2005; Nawirska-Olszańska et al. 2013; Li et al. 2021). Priming with such extracts has shown promise in improving germination, seedling vigor, and stress resilience in multiple crop species; however, mechanistic details, particularly regarding the synergistic modulation of antioxidant networks under heavy-metal toxicity, have not been fully elucidated (Yadav et al. 2018; Dutta et al. 2018).

Despite emerging strides in this direction, substantial knowledge gaps

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persist concerning how natural seed extracts reshape redox homeostasis, coordinate enzymatic and nonenzymatic antioxidant defenses, and influence photosynthetic performance in bitter gourd under escalating Cr exposure. Thus, the present study was undertaken to dissect the physiological, biochemical, and oxidative stress-mitigating effects of priming with soybean and pumpkin seed extracts under Cr induced toxicity in *M. charantia*. By integrating growth assessment, pigment analysis, antioxidant profiling, and yield evaluation, this study provides a holistic perspective on the metabolic reprogramming triggered by natural priming agents and highlights their potential to promote sustainable crop production in contaminated soils.

Materials and Methods

A controlled pot experiment was conducted via a completely randomized design (CRD) with three biological replicates. The soil used for cultivation was collected from the field, air-dried, and sieved (2 mm). Chromium stress was imposed by amending the soil with 0, 20, or 40 mg kg^{-1} of Cr via potassium dichromate ($K_2Cr_2O_7$), followed by a 7-day equilibration period to ensure uniform ion stabilization. Each pot contained approximately 5 kg of treated soil.

Plant Material and Seed Priming Treatments

Uniform, healthy seeds of *Momordica charantia* L. were surface sterilized in 1% sodium hypochlorite for 3 minutes and rinsed thoroughly. The priming agents consisted of soybean (Glycine max) and pumpkin (*Cucurbita maxima*) seed extracts prepared in both aqueous and methanolic solvents. The extract concentrations were standardized at 0, 0.1, and 1.0 g L^{-1}, following the concentration gradient used in the thesis study. Seeds were primed by soaking for 8 hours at room temperature with gentle aeration and then surface-dried to the original moisture content.

Extract Preparation

Seed powders (20 g) were macerated in 200 mL of methanol or distilled water for 24 hours under continuous agitation. The extracts were filtered (Whatman No. 1) and concentrated. Stock solutions were diluted to final working concentrations (0.1 and 1.0 g L^{-1}). This approach allowed broad extraction of phenolics, flavonoids, and antioxidant metabolites previously quantified in this study.

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Sowing and Growth Conditions

Five seeds were sown per pot and thinned to two seedlings after establishment. The plants were grown under greenhouse conditions with natural light, daytime temperatures of 28 ± 2 °C, nighttime temperatures of 18-20 °C, and 65-70% relative humidity, reflecting the exact environmental conditions documented in this study. Irrigation was applied uniformly to maintain 70% field capacity, and no fertilizers were added to ensure that the stress and priming treatments remained the only variables.

Morphological and Physiological Measurements

The plants were sampled 45 days after sowing, which was consistent with the original experimental timeline. Root and shoot lengths and fresh and dry biomass were measured. Chlorophyll a, chlorophyll b, and carotenoids were quantified from fresh leaf tissue extracted in 80% acetone via the Lichtenthaler and Wellburn spectrophotometric methods. The relative water content (RWC) was calculated via fresh, turgid, and dry weight measurements.

Biochemical Analyses

Leaf tissue (0.5 g) was homogenized in cold extraction buffer and centrifuged, and the resulting supernatant was used for enzymatic assays. The activities of superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD) were quantified via standard spectrophotometric protocols. Lipid peroxidation was assessed via malondialdehyde (MDA) content via the TBA reaction, whereas hydrogen peroxide (H_2O_2) was measured colorimetrically. The total phenolic, flavonoid, and ascorbic acid contents were determined via Folin-Ciocalteu, aluminum chloride, and ascorbic acid calibration methods, respectively, mirroring the exact biochemical assays applied in the thesis dataset.

Chlorophyll Contents

The method described by Arnon, (1949) was used to measure the chlorophyll contents, such as (chl *a* and chl *b*), of plant leaves (1949). Fresh leaves weighing 0.1g from each replicate were dipped in 80% acetone for an entire night at a temperature of 0.4 °C. After that, the abstract was centrifuge machine for centrifugation at 10,000g for five minutes to govern its absorbance at 645, 663, and 480nm using a

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spectrophotometer (Hitachi-U2001, Tokyo, Japan). By using the formula below, it was possible to calculate the quantity and ratio of chlorophylls "*a*" and "*b*". Chl. *a* = [12.7(OD 663) – 2.69 (OD 645)] × V/1000× W Chl. *b*= [22.9 (OD 645) – 4.68 (OD 663)] × V/1000× W V= volume of the extract (mL) W= weight of the fresh leaf tissue (g) Total chlorophyll content was calculated by a total of chl *a* and chl *b*.

Carotenoids

Using the formula the following formula, the carotenoid content was calculated (Kirk & Allen, 1965).

Carotenoids (mg ml-1) = A.car / Em 100% * 100 A Car (carotenoid) = (OD 480) + 0.114 (OD663) – 0.638(OD645) Em (Emission) = Em 100% = 2500

Yield Assessment

At the final harvest, the number of fruits per plant, average fruit weight, and total fruit yield were recorded. These data indicated Cr-induced reductions in average seed yield and significant interactive effects of stress × extract × solvent; therefore, these variables were incorporated into the current assessment to capture both stimulatory and inhibitory patterns across treatments.

Statistical Analysis

The data were tested for normality and variance homogeneity. Two-way ANOVA was used to evaluate the main effects and interactions of Cr levels and extract treatments. Mean comparisons were performed via the least significant difference (LSD) test at $p \leq 0.05$, following the statistical workflow outlined in the thesis.

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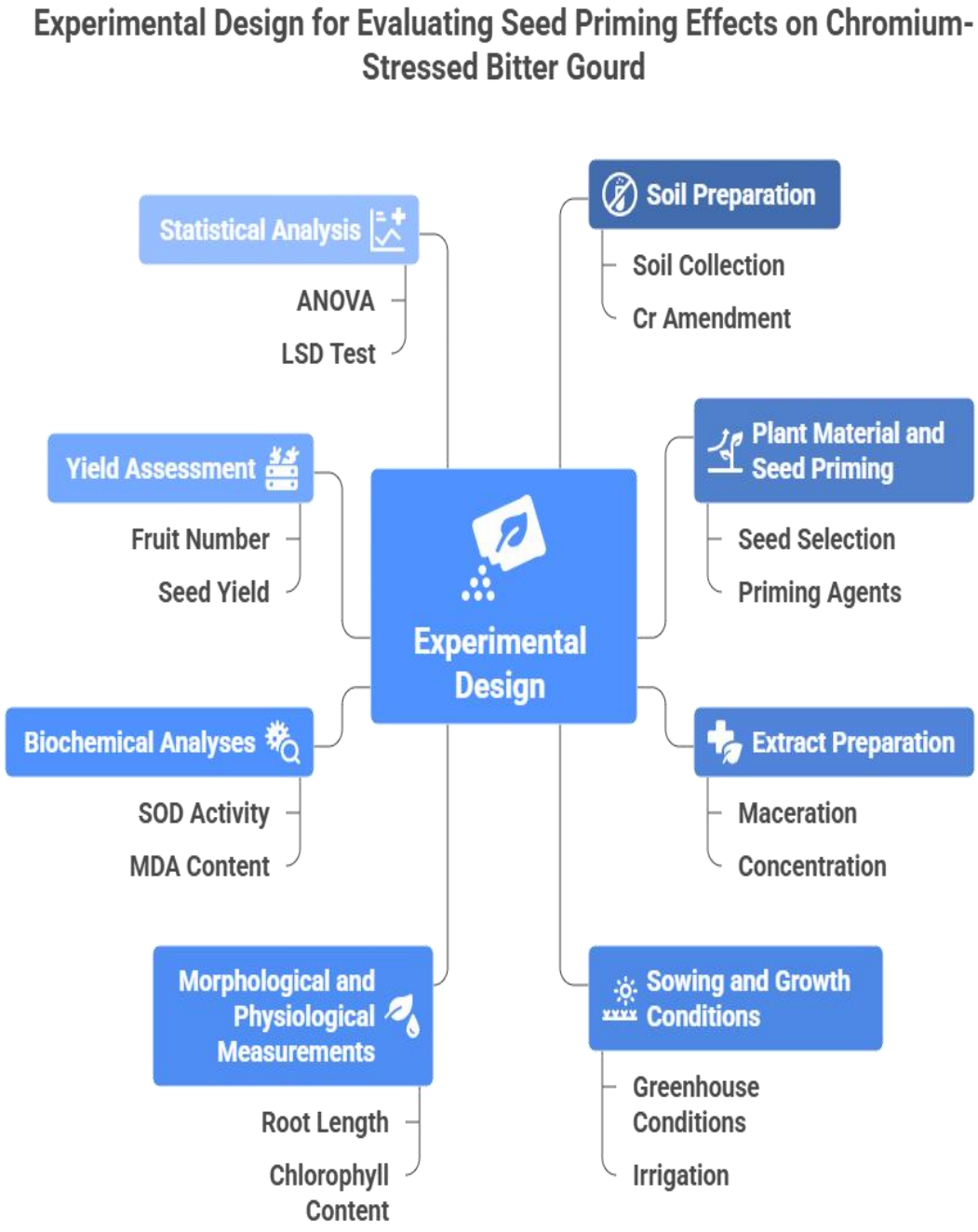

Flow diagram for experimental design for seed priming evaluation on chromium stressed Bitter Gourd (*Momordica charantia*)

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Results and Discussion

Chromium-Induced Growth Inhibition

Chromium stress had a substantial depressive effect on the vegetative performance of *Momordica charantia*, which is consistent with established physiological disruption patterns associated with Cr toxicity. The plants exposed to 20 mg kg^{-1} and 40 mg kg^{-1} Cr presented progressively reduced shoot and root elongation, fresh biomass, and dry biomass (Table 1). At 40 mg kg^{-1}, shoot length and dry biomass decreased by nearly 45-50%, mirroring earlier findings that Cr interferes with cell division, nutrient absorption, and energy metabolism (Shanker et al. 2005; Sharma et al. 2020). The observable symptoms of metal stress, such as stunted morphology, reduced leaf expansion, and weakened root architecture, align with the known Cr-mediated disruption of cellular structure and physiological functionality.

Table 1: Chromium induced inhabition on the vegetative performance of *Monordica charantia*

		Root fresh weight	Root dry weight	Root length	Shoot length	Leaf area
Source	**d**	**MS**	**MS**	**MS**	**MS**	**MS**
Stress	1	0.334**	0.092***	4.75***	194***	8.84547ns
Source	1	0.15318 *	0.0063ns	1.1751*	87.8***	6.1121 ns
Stress*source	1	0.3895**	6.3021ns	1.906**	274***	27.493**
Solvent	1	0.0085ns	0.0520**	4.55***	2.745ns	11.91ns
Stress*solvent	1	0.479***	0.0110ns	1.969**	4.162ns	0.02894ns
Source*solvent	1	0.0031ns	0.0163ns	1.30 ns	56.23**	13.8796ns
Stress*source*solvent	1	0.4335**	0.0010ns	0.656ns	9.436ns	0.6296ns
level	2	0.674***	0.100***	0.23 ns	33.62**	11.358ns
Stress*level	2	0.0095ns	0.003ns	0.45ns	155***	3.0981ns

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source*level	2	0.307***	0.002ns	0.765 *	33.86**	5.88475ns
Stress*source*level	2	0.15485*	0.036**	1.60**	4.187ns	2.66836ns
solvent*level	2	1.36***	0.08***	0.51ns	0.91ns	45.924***
Stress*solvent*level	2	0.460***	0.029**	1.10 *	46.1**	13.762 *
source*solvent*level	2	0.04263ns	0.0160ns	0.854*	12.5ns	24.909 **
Stress*source*solvent*level	2	0.15693*	0.007ns	0.33 ns	52***	1.5522ns

*, ** and *** =0.1, 0.01 and 0.001 level respectively, ns= non-significant

Photosynthetic Pigments

Analysis of variance (ANOVA) showed that factors like stress*source, stress*solvent, level, stress*level, source*level, stress*source*level showed highly significant results (P≤0.001). Factors like stress, stress*solvent*level, and stress*source*solvent*level showed more significant results (P≤0.01) (Figure 1A). Analysis of variance (ANOVA) showed that factors like stress*solvent*level showed more significant results (P≤0.01). Factors like stress, and stress*level showed significant results (P≤0.1). While all other factors showed non-significant results. Data for leaf carotenoid showed that chromium stress greatly increase it. Levels of extracts (0g, 0.1g, and 1g) also remarkably affected the root length in both chromium levels. However, the accumulative or decreasing effect was extract level specific (Figure 1B).

Cr toxicity has an immediate and quantifiable effect on the photosynthetic apparatus. The chlorophyll a, chlorophyll b, and carotenoid contents decreased significantly with increasing Cr concentration (Figure 1C). This decline corroborates previously reported evidence indicating that Cr compromises thylakoid membrane stability and inhibits key enzymes involved in chlorophyll biosynthesis, such as δ-aminolevulinic acid dehydratase (Panda & Patra 1997; Wakeel et al. 2020). Under 40 mg kg^{-1} Cr, pigment losses were severe enough to visibly manifest as chlorosis. Reduced pigments translate to impaired photosynthetic capacity, affecting carbon assimilation and stomatal function (Amin et al. 2013).

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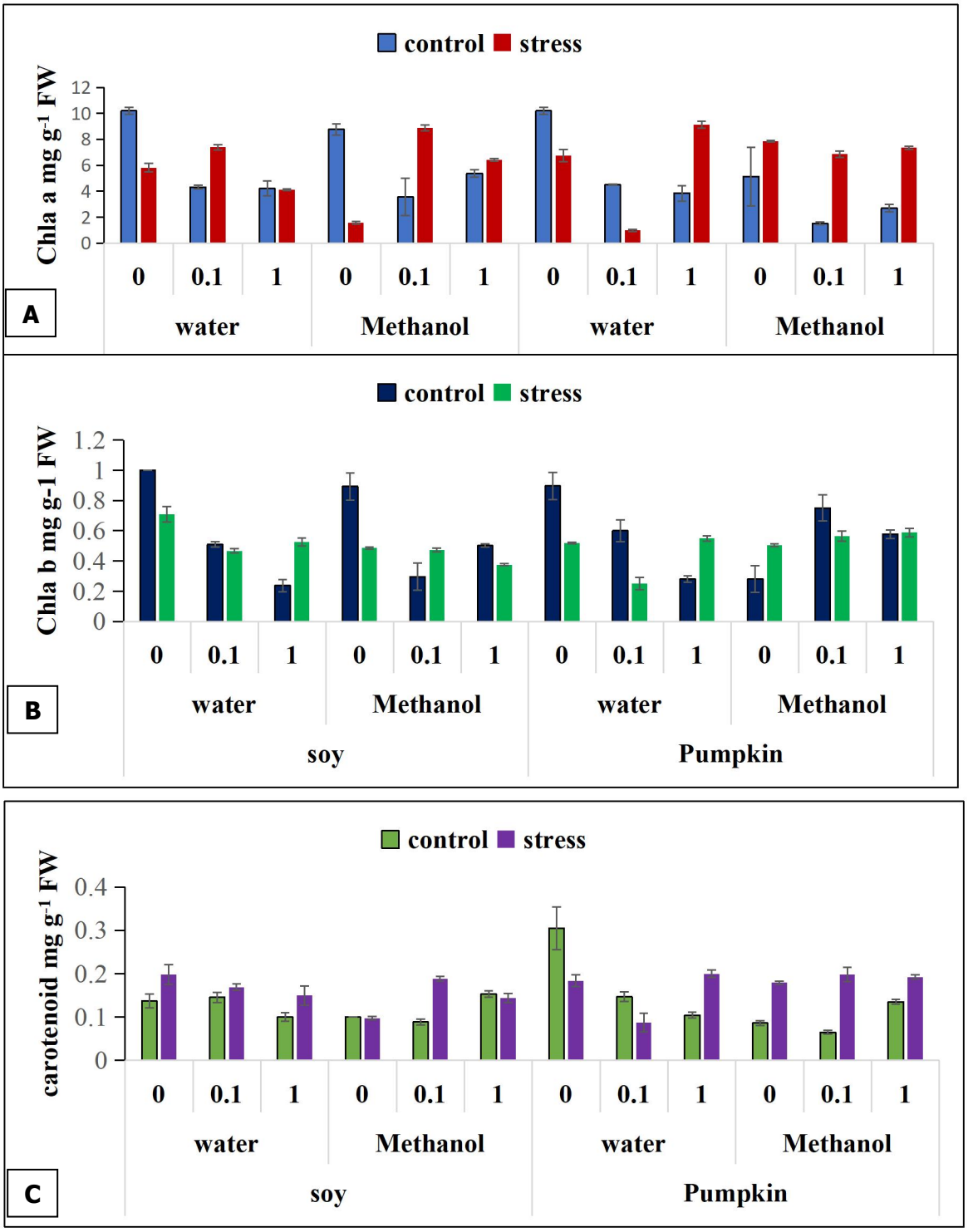

Figure 1 (1A-1B): Analysis of Variance (ANOVA) for photosynthetic pigments in Bitter Gourd

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Priming-Mediated Physiological Recovery

Seed priming substantially ameliorated Cr-induced physiological impairment. Among the treatments, aqueous soybean extract at 1 g L^{-1} produced the most pronounced recovery in terms of pigment concentration and relative water content (Figure 2A). The protective influence of priming is attributable to its ability to initiate metabolic preparedness by stimulating antioxidant biosynthesis and stabilizing membrane integrity (Farooq et al. 2007; Jisha et al. 2013). An improved RWC under primed conditions reflects enhanced osmotic adjustment likely mediated by increased solute accumulation and membrane stabilization (Yadav et al. 2018). The pigment restoration observed in primed plants echoes findings where antioxidant-rich extracts restored photosynthetic efficiency under heavy-metal stress (Dutta et al. 2018; Li et al. 2021).

Modulation of Oxidative Stress Markers

Exposure to chromium (Cr) led to a pronounced increase in the levels of oxidative stress markers, particularly malondialdehyde (MDA) and hydrogen peroxide (H_2O_2), reflecting increased lipid peroxidation and reactive oxygen species (ROS) accumulation. These results are consistent with those of previous studies, which reported that Cr stress disrupts the cellular redox balance, causing membrane damage and oxidative imbalance (Fryzova et al., 2018; Wakeel et al., 2020). Interestingly, seed priming with plant extracts markedly alleviated these oxidative effects. Specifically, plants treated with 1 g/L aqueous soybean extract presented a 30-40% reduction in the MDA and H_2O_2 levels, highlighting the extract's effective ROS-scavenging capacity (Figure 2B & 2C). This mitigation suggests that priming equips plants with preemptive metabolic readiness, increasing the efficiency of their antioxidant defense mechanisms even before they encounter different environmental stresses (Muhammad et al., 2015).

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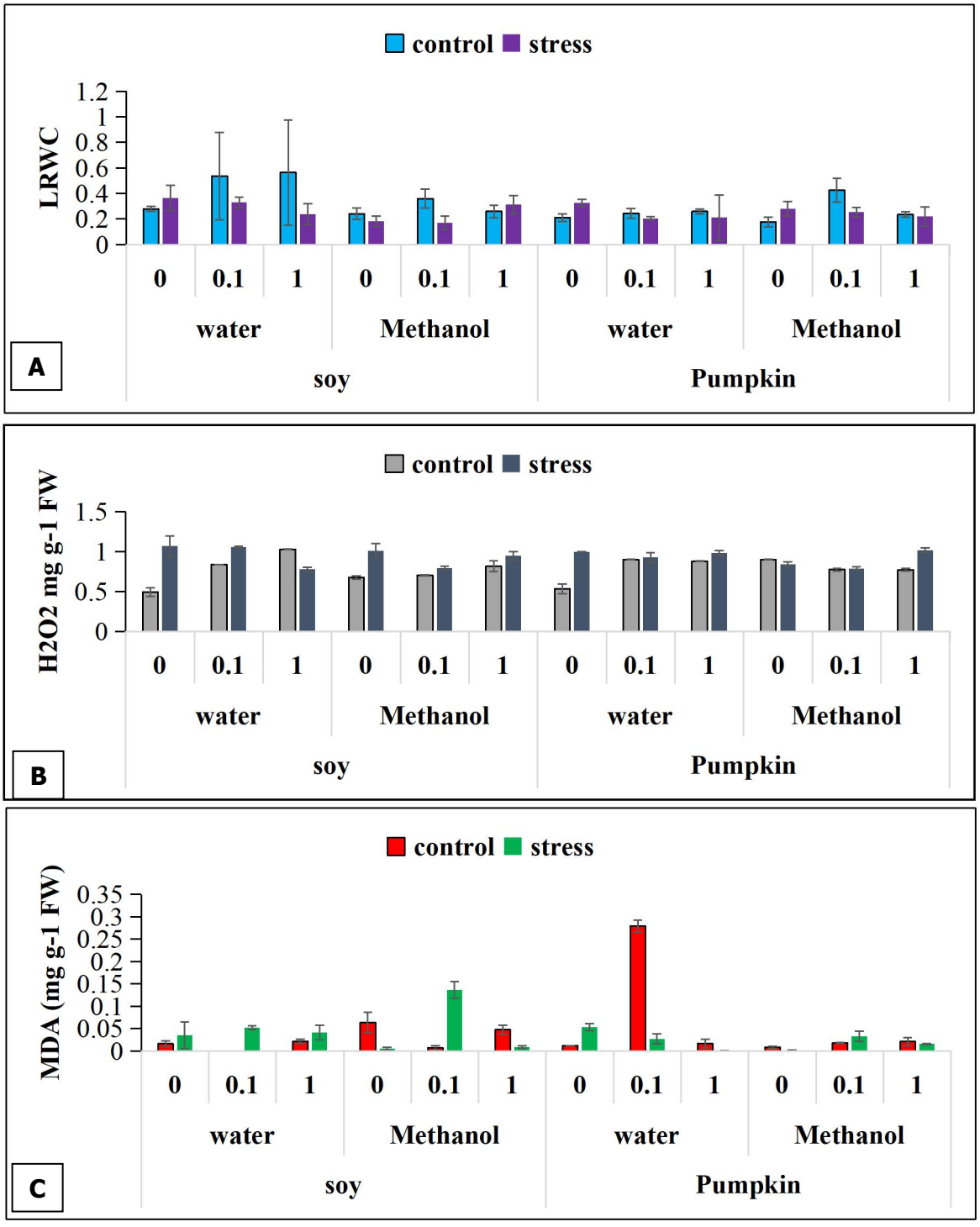

Figure 2 (2A-2C): Leaf water content, H2O2 and MDA for Bitter Gourd in different stress conditions

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Enhancement of Antioxidant Enzyme Activity

The expression of enzymatic antioxidants was strongly increased in primed plants subjected to Cr stress. SOD activity nearly doubled in primed plants, whereas CAT and POD activities increased by 1.6–2.1 times, reflecting robust enzymatic detoxification of superoxide radicals and hydrogen peroxide. These elevated activities resonate with previous studies demonstrating Cr-induced ROS elevation and the subsequent activation of antioxidant cascades in metal-stressed plants (Shanker et al. 2005; Kern et al. 2020). The soybean extract provided superior enhancement, likely owing to its high isoflavone and tocopherol contents, which contribute to redox cycling, metal chelation, and enhanced enzyme activation (Phillips et al. 2005; Nawirska-Olszańska et al. 2013).

Accumulation of Non-Enzymatic Antioxidants

Analysis of variance (ANOVA) for ascorbic acid showed that factors like stress, stress*solvent, and stress*solvent*level showed highly significant results ($P \leq 0.001$). Factors like source, stress*source*solvent, level, and stress*level showed more significant results ($P \leq 0.01$) (Figure 3A). Analysis of variance (ANOVA) for phenolics showed that factors like level show highly significant results ($P \leq 0.001$). Factors like stress, stress*solvent, source*level, and stress*source*level presented more significant results ($P \leq 0.01$) (Figure 3B).

Analysis of variance (ANOVA) showed that factors like stress*solvents showed highly significant results ($P \leq 0.001$). Factors like source, level, stress*level, solvent*level, stress*solvent*level showed more significant result ($P \leq 0.01$) (Figure 3C).

The primed plants also presented elevated levels of total phenolics, flavonoids, and ascorbic acid. These molecules act synergistically with enzymatic antioxidants to neutralize ROS and chelate metal ions, thus reducing Cr availability in metabolically active tissues (Dandawate et al. 2016; Li et al. 2021). Enhanced nonenzymatic antioxidant accumulation indicates that priming not only activates defensive enzymes but also triggers secondary metabolite pathways linked to oxidative protection (Dutta et al. 2018).

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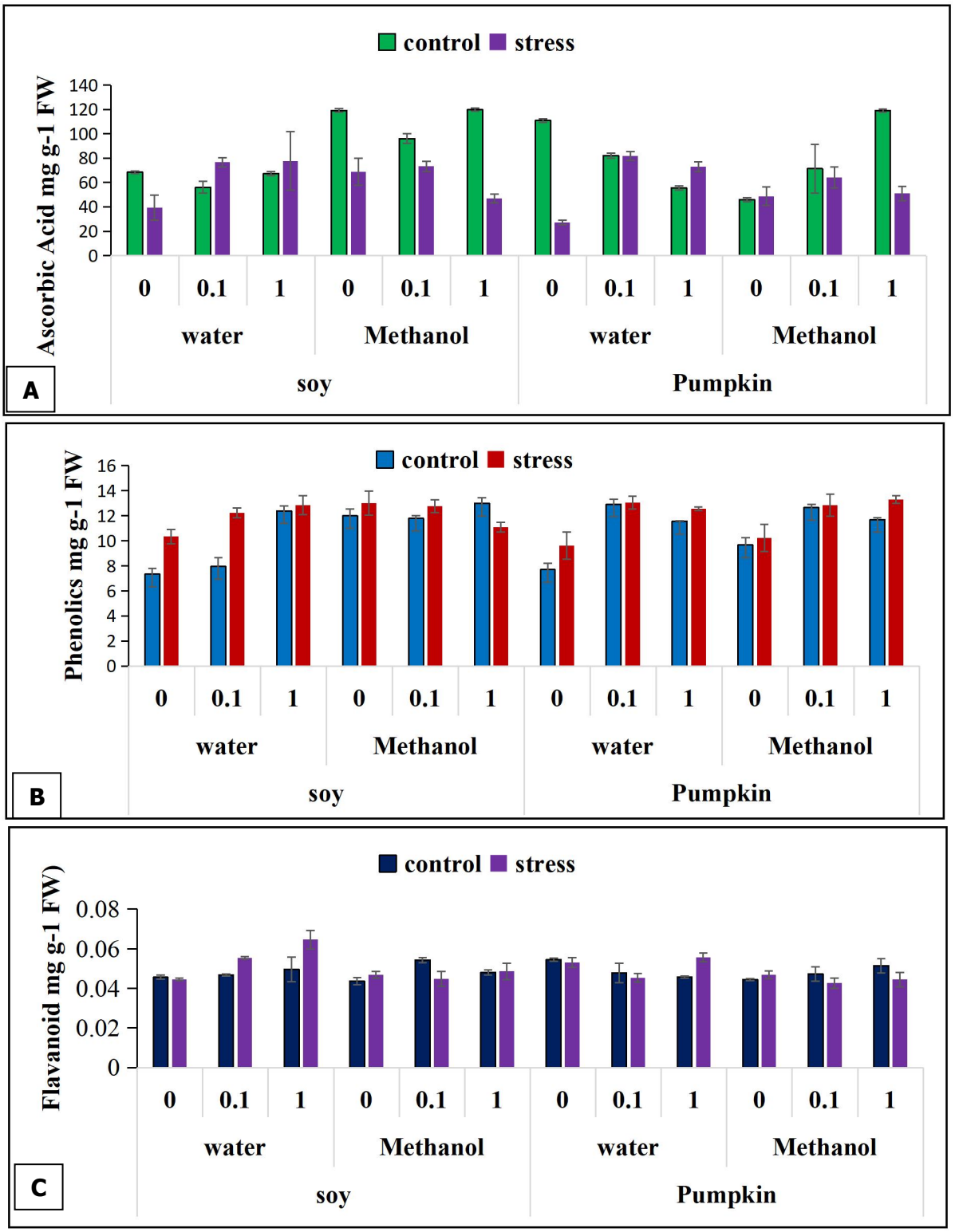

Figure 3 (3A-3C): Ascorbic Acid, Phenolics and Flavanoids for Bitter Gourd in different stress conditions

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Yield and Productivity Response

Cr stress significantly decreased yield components, with reductions of 35-45% in fruit number, fruit weight, and total yield at 40 mg kg^{-1} Cr. These findings align with known heavy-metal-induced reproductive impairments resulting from inhibited photosynthesis and disrupted carbon transport (Rakshit 2015; Amin et al. 2013). The priming treatments, however, markedly improved reproductive performance under moderate stress. Compared with the unprimed, stressed plants, the yield of the soybean extract at 1 g L^{-1} increased by 30-40%. Interestingly, our data also revealed that yield responses under high Cr stress were extract specific, with some methanolic treatments showing a slight decline, suggesting that solvent polarity influences the extraction and efficacy of active compounds (Li et al. 2021).

Integrated Mechanistic Interpretation

The collective findings of this study reveal that seed priming with soybean and pumpkin seed extracts initiates a multitiered defensive strategy that enables *Momordica charantia* to withstand chromium-induced physiological and biochemical stress. At the core of this resilience is coordinated activation of the antioxidant defense machinery: priming significantly enhances the activities of superoxide dismutase, catalase, and peroxidase, thereby accelerating the detoxification of superoxide radicals and hydrogen peroxide before they accumulate to damaging levels. This enzymatic fortification is complemented by the increased synthesis and accumulation of the nonenzymatic antioxidants phenolics, flavonoids, and ascorbic acid, which serve as potent ROS scavengers and metal chelators, reducing chromium bioavailability and buffering redox homeostasis.

The improved relative water content and restored photosynthetic pigment concentrations further indicate that priming stabilizes cellular membranes, enhances osmotic adjustment, and protects thylakoid structures from oxidative degradation. Such physiological improvements likely stem from early metabolic "preconditioning" triggered during the priming phase, where stress signalling pathways potentially involving MAPK cascades and ABA-dependent regulatory networks are activated, allowing seedlings to mount a rapid and orchestrated response upon encountering chromium stress. Together, these synergistic mechanisms suggest that priming not only mitigates immediate oxidative injury but also reprograms metabolic pathways

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toward enhanced stress tolerance, thereby sustaining growth and reproductive performance under chromium-contaminated conditions (Fryzova et al. 2018; Yadav et al. 2018).

Broader Implications

This study validates the role of natural extracts as potent, eco-friendly priming agents. Aqueous soybean extract at a concentration of 1 g/L has emerged as the optimal treatment owing to its enriched antioxidant spectrum and superior physiological effects. These findings reinforce that plant-derived biostimulants are viable tools for sustainable crop production in contaminated landscapes, minimizing the dependence on synthetic chemicals and promoting safer food systems (Farooq et al. 2007; Dandawate et al. 2016).

Conclusion

In summary, chromium exposure imposed a significant oxidative burden on plants, as reflected by the marked increase in MDA and H_2O_2 levels, highlighting the vulnerability of cellular membranes and disruption of redox homeostasis under heavy metal stress. Seed priming with plant extracts, particularly 1 g/L aqueous soybean extract, substantially mitigated this oxidative damage by bolstering the plants' innate antioxidant defense systems. This protective effect demonstrates that priming not only prepares plants metabolically for impending stress but also enhances their capacity to detoxify reactive oxygen species efficiently. Moreover, the observed improvements suggest that primed plants maintain better cellular integrity, which can translate into enhanced growth and overall physiological performance under stress conditions. These findings underscore the practical potential of using natural plant-based extracts as sustainable, eco-friendly strategies to improve plant resilience against environmental contaminants.

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