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Effects of Combined Glyphosate and Cadmium Stress on the Growth and Physiological Activity of Rhizobia

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***Abstract*—Glyphosate and cadmium (Cd) frequently co-occur in agricultural soils, yet their combined effects on rhizobia remain unclear. This study evaluated the synergistic impacts of different glyphosate and Cd concentrations on rhizobial growth and physiological responses. Growth performance was assessed by CFU counts, OD600, pH measurement, ICP-MS, oxidative stress assays, and SEM observation. Low-dose co-exposure (0.5 mg/L glyphosate + 0.5 mg/L Cd) promoted proliferation, increasing CFU by 20.93% and accelerating logarithmic growth. In contrast, high-dose treatment (2 mg/L + 2 mg/L) reduced CFU by 27.91%, decreased OD600, and induced morphological damage and oxidative imbalance. Treatments containing 2 mg/L Cd also reduced pH and increased Cd accumulation. These findings reveal concentration-dependent interactive effects under combined contamination.**

I. INTRODUCTION

Glyphosate is widely used in modern agriculture to improve crop yield, but its effects on soil microorganisms, especially rhizobia, remain insufficiently understood[1]. Combined contamination with glyphosate and cadmium (Cd), mainly derived from phosphate fertilizers, poses increasing environmental risks. High glyphosate concentrations significantly inhibit rhizobial growth, while optimal growth occurs at pH 5-8 and 20-30 °C[2]. Cd is a recognized environmental pollutant with high toxicity to microorganisms, and rhizobial IC_{50} values range from 3.06 to 7.5 mg/L[3,4]. Low-Cd soils may harbor more tolerant strains, possibly due to co-tolerance or phenotypic adaptations[5].

Rhizobia are bacteria that establish symbiotic relationships with legumes, forming root nodules and fixing atmospheric nitrogen. They produce plant hormones that promote root growth and development and enhance plant tolerance to environmental stresses such as drought and salinity. Inoculation with rhizobia can improve the yield and quality of legume crops, reduce nitrogen fertilizer application, lower production costs, and contribute to environmental protection. In ecological restoration of degraded lands, planting legumes inoculated with rhizobia increases soil nitrogen content, improves soil structure, and facilitates vegetation recovery[6]. Glyphosate is a broad-spectrum, non-selective, systemic organophosphorus herbicide. It is a white solid, non-volatile, insoluble in common organic solvents but readily soluble in water. Absorbed via plant stems and leaves, it translocates throughout the plant, inhibiting 5-enolpyruvylshikimate-3-phosphate synthase (EPSPS) and disrupting protein synthesis, ultimately causing plant death[7]. Recognized as one of the most important and successful herbicides due to its high physical and chemical stability, excellent efficacy, and low cost, it is widely applied in agricultural and non-agricultural areas to control annual and perennial weeds. Residual glyphosate in soil not only impairs plant growth but also disrupts soil microbial community structure and function[8], exerting significant adverse effects on various physiological and biochemical processes, including reduced photosynthetic efficiency, accelerated chlorophyll degradation, inhibited chlorophyll function and iron reductase activity, disrupted auxin transport, and enhanced auxin oxidation[9]. Glyphosate inhibits the growth of beneficial soil microorganisms such as nitrogen-fixing bacteria and mycorrhizal fungi, while potentially promoting harmful ones, thereby altering soil microbial community structure and impairing ecological functions[10]. It also suppresses activities of soil enzymes including urease, phosphatase, and sucrase, disrupting nutrient transformation and cycling, and reducing soil fertility and sustainability[11]. At very low concentrations, cadmium may promote plant growth by enhancing antioxidant enzyme activities and stress tolerance[12]; altered root exudates in Cd-contaminated soils can facilitate symbiotic microbial relationships, indirectly benefiting plants, and certain bacteria exhibit enhanced degradation of organic pollutants due to Cd activation of intracellular enzymes. In contrast, high Cd concentrations inhibit seed germination, seedling growth, root elongation, and lateral root formation, impair root development, disrupt chloroplast structure and function, reduce chlorophyll content and photosynthetic efficiency, and decrease organic matter accumulation[13]. Cadmium crosses the blood-brain barrier, impairing neuronal function and causing behavioral abnormalities, motor incoordination, and sensory deficits in animals[14]. This study investigates the synergistic effects of glyphosate and cadmium (Cd) from the perspective of combined pollution, using rhizobia (root nodule bacteria) as the model organism. It examines whether co-exposure to glyphosate and Cd exerts toxic effects on rhizobia, thereby elucidating the impacts of binary pollutant contamination on rhizobial growth and activity.

II. EXPERIMENTAL

A. Bacterial culture

Using a 50 μL pipette, aspirate the generation 0 (G0) rhizobial culture and inoculate it into the liquid medium. Incubate with shaking at 30°C and 120 r/min for 48 h. Take a small aliquot of the cultured bacterial suspension and streak it onto the surface of solid medium using the streak plate method. Invert the plates and incubate at 30°C in a constant-temperature incubator. Repeat the above procedure to perform 3-4 successive subcultures (generations).

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Using a pipette, transfer 50 μL of rhizobial culture to inoculate fresh liquid medium and incubate at 30°C for 24 h. Then, take 50 μL of this preculture and inoculate it separately into the blank control group and different pollutant treatment group liquid media. Continue incubation at 30°C for 72 h to prepare the working cultures.

B. Concentration settings

Based on a review of relevant literature, four combinations of glyphosate and cadmium concentrations, along with a blank control group (five concentration combinations in total), were established and configured as follows: 0 mg/L glyphosate + 0 mg/L cadmium (blank control group without added test substances), 0.5 mg/L glyphosate + 0.5 mg/L cadmium, 0.5 mg/L glyphosate + 2 mg/L cadmium, 2 mg/L glyphosate + 0.5 mg/L cadmium, and 2 mg/L glyphosate + 2 mg/L cadmium.

C. Determination of Heavy Metal Ion Content

The high-concentration cadmium standard stock solution was diluted with ultrapure water to prepare a series of standard working solutions. An aliquot of the sterilized and filtered bacterial sample was taken, and its volume was recorded. A 30% (v/v) nitric acid solution was prepared by diluting concentrated nitric acid to a total volume of 1000 mL. The bacterial sample was diluted 100-fold with this 30% nitric acid solution, filtered, and then aliquoted into three parallel replicates. The standard working solutions were first introduced into the inductively coupled plasma mass spectrometer (ICP-MS) to measure the cadmium signal intensity under the established instrument conditions, followed by analysis of the processed sample solutions using the same parameters.

D. Oxidative Stress Experiment

Eight milliliters of bacterial suspension were separately taken from the blank control group and the treatment group containing 2 mg/L glyphosate combined with 2 mg/L cadmium, and transferred into 10 mL centrifuge tubes. The samples were centrifuged at 6000 r/min for 5 min, and the supernatant was discarded. The pellet was resuspended in 8 mL of deionized water, followed by homogenization and grinding. The resulting cell homogenate was used to determine the levels of superoxide dismutase (SOD), malondialdehyde (MDA), and reduced glutathione (GSH) in the bacteria, according to the recommended procedures provided in the respective assay kits for SOD, MDA, and GSH.

E. Determination of Bacterial Physiological Functions

A 25 μL aliquot of the 72-h cultured bacterial suspension was transferred into 10 mL of sterile water and thoroughly mixed to achieve the first dilution. Subsequently, 50 μL of this diluted suspension was added to another 10 mL of sterile water for the second dilution. Then, 50 μL of the twice-diluted bacterial suspension was pipetted onto the surface of solid medium, spread evenly, and the plates were incubated at 30°C for 48 h. A 50 μL aliquot of 24-h cultured rhizobial suspension was inoculated into liquid medium containing the designated pollutant concentrations. Immediately after inoculation, the initial optical density (OD) of the culture was measured at 600 nm using a UV-visible spectrophotometer, and the value was recorded. The cultures were then placed in a vertical incubator. Thereafter, OD_{600} was measured every 12 h under the same conditions until 72 h of incubation.

F. Data Processing and Statistical Analysis

In this study, the mean was selected to represent the central tendency of all obtained data, and the standard deviation (SD) was used to reflect data variability. Results are expressed as mean ± SD.The Student's t-test was employed as the primary statistical method to compare the means of two independent samples. By calculating the exact t-value, it was determined whether the two groups originated from populations with the same mean. In the context of this study, the control group and each treatment group were treated as two independent samples, and Student's t-tests were performed individually for each measured parameter to identify potential differences in means between groups.

III. RESULTS AND DISCUSSION

A. pH and Cadmium Concentrations in Different Culture Environment

Rhizobial growth and metabolic activity are influenced by pH; values outside the optimal range may inhibit bacterial proliferation and, in severe cases, cause cellular damage or death. In this study, the pH of the bacterial suspension after combined exposure to glyphosate and cadmium was measured, as shown in Figure 1. The results indicate that the pH of rhizobial cultures under combined glyphosate and cadmium stress remained within the slightly alkaline range (pH 7-13) suitable for normal rhizobial metabolism[15]. This suggests that rhizobia can maintain an appropriate growth and metabolic environment through physiological self-regulation in response to adverse external conditions.

Further comparison revealed that the blank control group exhibited the highest pH, followed by the 0.5 mg/L glyphosate + 0.5 mg/L cadmium group and the 2 mg/L glyphosate + 0.5 mg/L cadmium group, while the lowest pH was observed in the 2 mg/L glyphosate + 2 mg/L cadmium treatment. Notably, significant pH reductions occurred in the 0.5 mg/L glyphosate + 2 mg/L cadmium group and the 2 mg/L glyphosate + 2 mg/L cadmium group. This decline may result from the combined inhibitory effects of high cadmium and glyphosate concentrations on rhizobial respiration or other metabolic processes, thereby altering the microorganisms' capacity to transform acid-base substances in the medium. Alternatively, the pollutants may promote the release or accumulation of certain acidic compounds, leading to decreased pH.

Under combined exposure in rhizobial culture, both glyphosate and cadmium concentrations changed over time. Previous studies have shown that glyphosate can alter the surface charge properties and functional group structures of solid particles, thereby affecting the adsorption-desorption equilibrium of cadmium[16]. The complexation between glyphosate and cadmium strengthens with increasing cadmium concentration, converting more adsorbed cadmium into free (dissolved) forms and elevating the soluble cadmium concentration in the medium, which in turn increases its potential toxicity to rhizobia and other organisms.

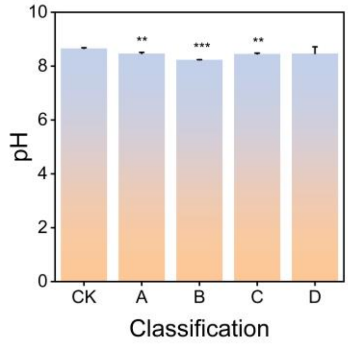

Figure 1. The pH of the bacterial solution in different pollutant treatment groups. (n=3). * p < 0.05 compared with the control group.CK:0mg/L GLY+0mg/L Cd; A:0.5mg/L GLY+0.5mg/L Cd; B:2mg/L GLY+0.5mg/L Cd; C:0.5mg/L GLY+2mg/L Cd; D:2mg/L GLY+2mg/L Cd

The cadmium concentrations measured in the bacterial suspensions after 72 h of combined exposure are presented in Figure 2. As expected, the control group showed nearly zero cadmium. Among the treatment groups, those initially containing 2 mg/L cadmium exhibited higher final cadmium concentrations. At the same initial cadmium concentration, higher glyphosate levels resulted in lower measured cadmium concentrations: compared with the 0.5 mg/L glyphosate + 0.5 mg/L cadmium group, the 2 mg/L glyphosate + 0.5 mg/L cadmium group showed an 8.5% reduction in cadmium concentration; similarly, the 2 mg/L glyphosate + 2 mg/L cadmium group exhibited a 5.3% reduction compared with the 0.5 mg/L glyphosate + 2 mg/L cadmium group. These findings indicate that glyphosate can form complexes with cadmium ions, thereby reducing the concentration of free cadmium in solution.

Overall, the results demonstrate the complex environmental effects of combined glyphosate and cadmium exposure. In terms of pH, high-concentration cadmium combined with glyphosate disrupts the acid-base balance of the medium. In terms of cadmium bioavailability, their interaction increases the proportion of free (bioavailable) cadmium. These two changes are interrelated: alterations in pH further influence the chemical speciation of cadmium and the growth conditions of microorganisms. Collectively, the combined pollution of glyphosate and cadmium perturbs multiple aspects of soil ecosystem stability, adversely affecting the habitat of soil microorganisms such as rhizobia and potentially impairing their nitrogen-fixing activity.

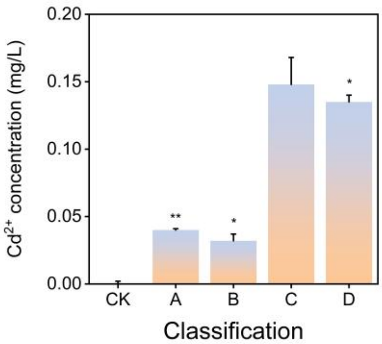

Figure 2. The cadmium concentration of the bacterial solution in different pollutant treatment groups. * p <0.05 compared with the control group.

B. Effects of Combined Glyphosate and Cadmium Exposure on Rhizobial Colony Counts

To investigate the synergistic effects of glyphosate and cadmium on rhizobial growth, 50 μL of bacterial suspension was inoculated into liquid media containing various concentration combinations of glyphosate and cadmium, followed by incubation for 72 h and subsequent determination of colony-forming units (CFU) via plate counting.

As shown in Figure 3, clear differences were observed among treatment groups. The 0.5 mg/L glyphosate + 0.5 mg/L cadmium group exhibited the highest colony counts, reaching approximately 5.2×10^7 CFU, representing a 20.93% increase compared to the control group. Contrary to the initial hypothesis that all pollutant treatments would inhibit rhizobial growth, low-concentration combinations instead promoted proliferation.

The 0.5 mg/L glyphosate + 2 mg/L cadmium group showed colony counts of about 4.3×10^7 CFU, similar to the control, indicating no significant synergistic toxicity at this combination. The 2 mg/L glyphosate + 0.5 mg/L cadmium group displayed a 9.30% increase over the control, suggesting a weaker promotional effect than the lower glyphosate-cadmium pair.

In contrast, the highest concentration group (2 mg/L glyphosate + 2 mg/L cadmium) reduced colony counts to 3.1×10^7 CFU, a 27.91% decrease relative to the control, demonstrating clear inhibitory effects under high combined pollution.

These results highlight the complex, concentration- and combination-dependent impacts of pollutants on microbial growth. The significant promotion in the 0.5 mg/L glyphosate + 0.5 mg/L cadmium group suggests that low doses may stimulate certain metabolic functions or activate gene expression related to nutrient uptake and cell division, thereby enhancing colony proliferation. Supporting evidence indicates that low pollutant mixtures can upregulate energy-related genes in microbial cells, increasing energy availability for division and growth [17]. In this experiment, this concentration pair likely enhanced nutrient acquisition and utilization efficiency via a similar mechanism, accelerating cell division and markedly increasing CFU.

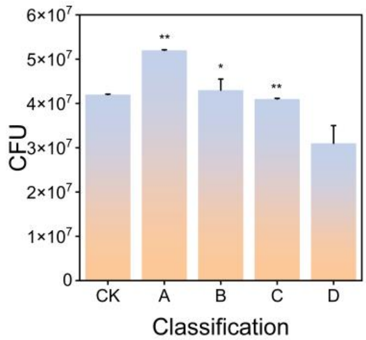

Figure 3. The number of colonies in different pollutant treatment groups. * p <0.05 compared with the control group.

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The 2 mg/L glyphosate + 0.5 mg/L cadmium group showed a mild promotional trend but lacked statistical significance, possibly because the concentrations lie in a transitional zone where stimulatory effects from low-level exposure coexist with emerging toxicity, resulting in antagonistic interactions and limited net promotion.

Due to the robust adaptive capacity of microorganisms, the 0.5 mg/L glyphosate + 2 mg/L cadmium group maintained CFU levels comparable to the control. However, high concentrations (2 mg/L glyphosate + 2 mg/L cadmium) exerted strong inhibition, causing multifaceted severe damage to microbial cells. At elevated levels, glyphosate potently suppresses enzyme activities, blocking amino acid and protein synthesis and thereby impairing growth and division. Cadmium, as a highly toxic heavy metal, binds strongly to intracellular proteins and enzymes at high concentrations, disrupting rhizobial structure and function.

Overall, the effects of glyphosate and cadmium on colony growth vary with concentration and combination: low doses may promote proliferation, high doses tend to inhibit it, and intermediate combinations allow microorganisms to regulate and sustain growth levels through adaptive mechanisms.

C. Effects of Combined Glyphosate and Cadmium on Rhizobial Growth

The growth curves of rhizobia in different pollutant treatment groups after 72 h of incubation are shown in Figure 4(a). During the initial phase (approximately 0-24 h), the OD_{600} values of all treatment groups increased slowly, with rhizobial growth remaining sluggish and differences among combinations being minimal. The growth trend was relatively flat during this lag phase.

Subsequently, OD_{600} values began to rise markedly as the cultures entered the logarithmic growth phase (approximately 24-60 h). In this phase, microbial metabolism is highly active, and cell numbers increase exponentially at a constant division rate. The 2 mg/L glyphosate + 0.5 mg/L cadmium group exhibited relatively faster growth in the later part of this phase compared to the control, whereas the 2 mg/L glyphosate + 2 mg/L cadmium group showed slower growth, indicating that high concentrations of the glyphosate-cadmium combination may inhibit rhizobial proliferation.

In the stationary phase (approximately 60-72 h and beyond), biomass in some treatment groups gradually reached a maximum, entering a state of dynamic equilibrium where growth rate equals death rate, and cell numbers no longer increased significantly. The 2 mg/L glyphosate + 0.5 mg/L cadmium group and the blank control group maintained relatively higher OD_{600} values during the stationary phase, corresponding to greater final biomass, while the 2 mg/L glyphosate + 2 mg/L cadmium group displayed lower OD_{600} values, further confirming the inhibitory effect of high combined concentrations on microbial growth and limiting final biomass.

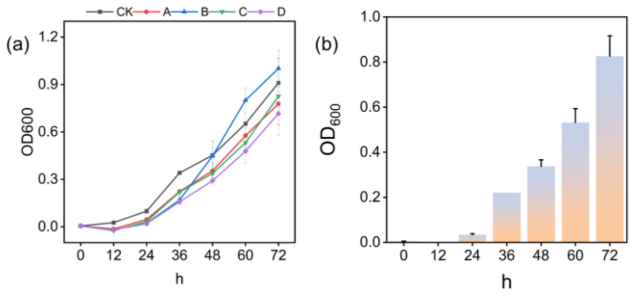

Figure 4. Growth curves of rhizobia under different pollutant treatment groups. (a) Growth curves from 0 to 72 hours; (b) Growth status at the 48-hour time point. * *p* <0.05 compared with the control group.

Overall, rhizobial growth was slow and showed little difference among treatments in the early phase (0-24 h). After 24 h, certain combinations (particularly 2 mg/L glyphosate + 0.5 mg/L cadmium) exhibited growth rates exceeding that of the control, suggesting that specific pollutant concentrations can promote rhizobial growth in later stages. In contrast, other combinations lagged behind. Thus, the influence of glyphosate and cadmium on rhizobial growth is time-dependent and concentration-combination-dependent, with distinct trends observed across different growth phases.

The bar graph in Figure 4(b), depicting OD_{600} values at 48 h of incubation, shows the following: the control group reached an absorbance of 0.55; the 0.5 mg/L glyphosate + 0.5 mg/L cadmium combination reduced absorbance to 0.45, indicating inhibition; the 2 mg/L glyphosate + 0.5 mg/L cadmium combination increased absorbance to 0.65, demonstrating a promotional effect; while the 0.5 mg/L glyphosate + 2 mg/L cadmium and 2 mg/L glyphosate + 2 mg/L cadmium combinations yielded absorbances of 0.30 and 0.35, respectively.

These results reveal that at 48 h of culture, combinations containing high cadmium concentrations generally inhibited rhizobial growth regardless of glyphosate level, except for the 2 mg/L glyphosate + 0.5 mg/L cadmium treatment, which showed promotion. The strongest inhibition was observed in the 0.5 mg/L glyphosate + 2 mg/L cadmium group. Collectively, the effects of glyphosate and cadmium on rhizobial optical density vary depending on concentration and combination, highlighting the need for additional experimental data to further validate these concentration-specific and interactive patterns.

D. Effects of Combined Glyphosate and Cadmium on Oxidative Stress in Rhizobia

This study demonstrates that the synergistic action of glyphosate and cadmium significantly alters the oxidative stress status of rhizobia. As shown in Figure 5(a), the protein concentration in the control group was approximately 0.75 g/L. When both glyphosate and cadmium concentrations were increased to 2 mg/L, the protein concentration markedly declined to about 0.25 g/L. In the control group, malondialdehyde (MDA) content was approximately 14 nmol/mg protein; under the 2 mg/L glyphosate + 2 mg/L cadmium treatment, MDA content decreased to about 10 nmol/mg protein, representing a reduction of approximately 66.7% relative to the control. As MDA is a primary product of

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lipid peroxidation, its decreased level indicates reduced oxidative damage to cellular membranes.

The high-concentration combination of glyphosate and cadmium exerted a pronounced inhibitory effect on rhizobial protein concentration, likely due to interference with metabolic pathways associated with protein synthesis. Glyphosate is known to inhibit key enzyme activities in microbial cells, thereby disrupting amino acid biosynthesis and subsequently impeding protein synthesis. Cadmium, as a heavy metal, can bind to intracellular proteins, disrupting their structure and function while accelerating protein degradation[18].

As illustrated in Figure 5(b), total superoxide dismutase (SOD) activity in the control group was approximately 190 U/mg protein. In the high-concentration (2 mg/L glyphosate + 2 mg/L cadmium) treatment group, total SOD activity decreased slightly to about 175 U/mg protein. In contrast, reduced glutathione (GSH) content in the control group was approximately 13 μmol/g, whereas it declined significantly to about 10 μmol/g in the 2 mg/L glyphosate + 2 mg/L cadmium group, with a statistically significant difference compared to the control.

The relatively minor impact on total SOD activity in the 2 mg/L glyphosate + 2 mg/L cadmium group suggests that, under the conditions of this experiment, SOD may not be the primary enzyme employed by rhizobia to counteract oxidative damage induced by high combined pollutant exposure. The significant reduction in GSH content indicates that the synergistic action of high-concentration glyphosate and cadmium depletes intracellular GSH reserves. This depletion reflects an elevated oxidative stress level in rhizobia under such stress, challenging the cellular antioxidant defense system and weakening the cell's capacity to resist oxidative injury.

Taken together, the oxidative stress indicators reveal that high concentrations of combined glyphosate and cadmium exert multifaceted adverse effects on rhizobia. In terms of protein metabolism, protein concentration is markedly reduced, impairing normal physiological functions. Regarding oxidative stress, MDA content is lowered (suggesting alleviated membrane lipid peroxidation), yet GSH content is significantly depleted, compromising the antioxidant capacity. These findings highlight the complex nature of the synergistic interaction at high concentrations: while lipid peroxidation is mitigated, the normal metabolism and synthesis of antioxidant enzymes and non-enzymatic antioxidants are simultaneously disrupted.

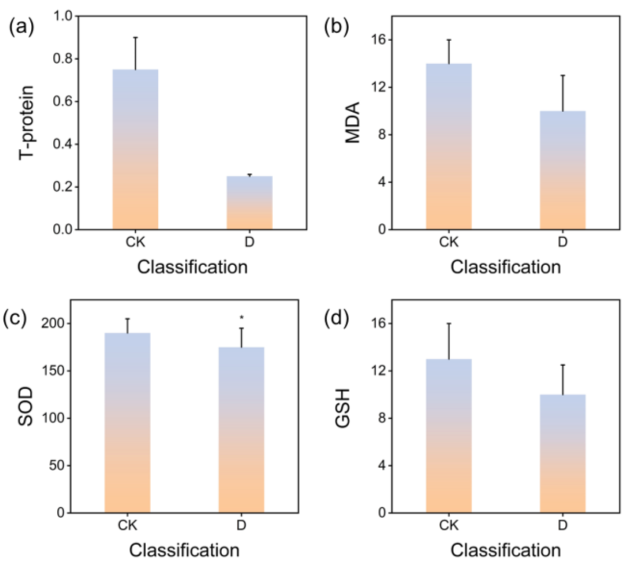

Figure 5. Oxidative stress parameters in rhizobia exposed to different pollutant treatments. (a) Total protein concentration; (b) Malondialdehyde (MDA) level as an indicator of lipid peroxidation; (c) Total superoxide dismutase (T-SOD) activity; (d) Glutathione (GSH) content. Asterisks indicate significant differences compared with the control group (*$p < 0.05$).

IV. CONCLUSION

This study demonstrates that combined exposure to glyphosate and cadmium exerts complex, concentration-dependent effects on rhizobial growth and activity: after 72 h, culture pH remains within the optimal neutral-to-alkaline range for rhizobial metabolism with suppression of acid accumulation most pronounced at 2 mg/L each, residual cadmium levels are significantly lower in treatments with higher glyphosate (2 mg/L) due to complexation, low concentrations (0.5 mg/L each) promote proliferation (CFU +20.93% vs. control) while high concentrations (2 mg/L each) strongly inhibit it (CFU -27.91%), certain combinations like 2 mg/L glyphosate + 0.5 mg/L cadmium enhance growth at 48 h (higher OD_{600}), high combined exposure causes severe cell rupture and morphological damage observed by SEM, and induces multifaceted oxidative stress characterized by sharply reduced protein concentration (~0.5 g/L drop), decreased MDA (~66.7% reduction indicating intensified lipid peroxidation damage), minor change in total SOD activity, and significant GSH depletion (~3 μmol/g), collectively compromising antioxidant defenses and potentially impairing nitrogen fixation in soil ecosystems.

V. ACKNOWLEDGMENT

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