Research Article

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Morphophysiological changes and reactive oxygen species metabolism in *Corchorus olitorius* L. under different abiotic stresses

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Abstract: Abiotic stress has become an alarming issue for plant survival due to the constant changes in the environment. Abiotic stresses such as drought, salt, waterlogging, and heavy metals largely influence plant growth and development that finally reduce crop productivity. The present study was carried out to investigate the responses of jute (*Corchorus olitorius* cv. O-9897) plant under different abiotic stresses. At 15th days after sowing plants were exposed to different abiotic stresses for various duration. Two doses of NaCl (200 and 400 mM) were applied to impose salt stress, while two doses of $CdCl_2$ (2 and 4 mM) were applied for cadmium (Cd) stress. Waterlogging stress was applied for 5 and 15 days. Whereas drought stress was imposed on plants for 10 and 15 days. Leaf relative water content, SPAD value, plant height, above ground fresh and dry weight, leaf area, and stem diameter decreased upon exposure to salt, water deficit, Cd, and waterlogging stresses. These abiotic stresses resulted in oxidative damage which was evident by the increased levels of lipid peroxidation, H_2O_2, and electrolyte leakage (EL) together with altered antioxidant enzymes activities and glyoxalase system which are crucial for plants to fight against oxidative damage. Both duration of waterlogging and drought stress drastically affected plant morphophysiology, whereas *C. olitorius* could tolerate moderate level of salt (200 mM NaCl) and Cd (2 mM $CdCl_2$). So the present study reveals that abiotic stresses cause substantial damages to the morphophysiology and oxidative stress tolerance of *C. olitorius* where the higher doses of NaCl and $CdCl_2$ as well as the increased duration of waterlogging and drought resulted in more deleterious effect.

Keywords: oxidative stress, salinity, waterlogging, metal toxicity, water deficit, antioxidant enzymes

1 Introduction

Stressful environmental conditions continuously create unfavorable conditions for plants and lead plants toward physiological and biochemical changes [1]. When plants are exposed to abiotic stresses such as drought, waterlogging, extreme temperatures, salinity, or metal/metalloid stresses plant growth, physiology, metabolism, productivity and every aspect of growth and development are negatively affected which can reduce yield up to 70% [2]. Plants produce excessive reactive oxygen species (ROS) in stress condition that damage membranes, photosynthetic apparatus, and different functional elements of plants [3]. Excess accumulation of ROS is marked as a stress indicator in plants which demolishes the balance between ROS production and activity of antioxidant defense system and causes cell damage in plants [4]. Hasanuzzaman et al. [5] stated that prolonged exposure to stress condition may cause cell death in plants. To avoid cell damage and death, plants increase the activities of antioxidant enzymes which is considered as one of the abiotic stress tolerance strategies of plants.

Jute (*Corchorus* spp.) is a tropical crop and cultivated mostly in Asia and African continents. Indo-Bangladesh subcontinent is considered as the best region for commercial jute cultivation [6]. Other major jute producing

Deceased.

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countries are China, Thailand, Myanmar, Indonesia, Brazil, and Nepal [7]. Due to alluvial type soil and sufficient rainfall, delta Ganga is considered as the best region for jute cultivation [8]. Though jute is a water loving plant at mature stage, at seedling stage it is sensitive to excess water stress and may be unable to complete its life cycle [9]. Salt stress reduces plant growth and affects germination to a great extent [10]. It also causes reduction in stem diameter which ultimately reduces yield and deteriorates fiber quality. Excess accumulation of ROS increases malondialdehyde (MDA) content and alters the activities of antioxidant enzymes [11]. Drought stress reduces leaf area of jute, decreases net photosynthesis rate, and causes growth reduction [12]. It also reduces fiber yield and produces low quality fiber [13]. When jute is exposed to cadmium (Cd) contaminated soil, physiological and biochemical processes of jute are adversely affected [14].

Though jute is one of the most important cash crop in Bangladesh and parts of India, there are very few literature regarding jute responses to different abiotic stresses. Therefore, this study has been conducted on the morpho-physiological and antioxidative responses of *C. olitorius* plant to various abiotic stresses viz., drought, salinity, Cd, and waterlogging.

2 Materials and methods

2.1 Plant materials and stress treatments

Healthy, matured, and uniform seeds of jute (*C. olitorius* cv. O-9897) were used for conducting the experiment. Seeds were sown in plastic pots (14 L) where organic manure, urea, triple super phosphate, and muriate of potash were used as per recommendation of Islam [15]. Thinning, weeding, and other intercultural operations were done when it was needed and 12 plants were allowed to grow per pot. At 15 days after sowing (DAS), plants were exposed in nine treatments viz., control, two doses of drought (10 days of water deficit; D_1 and 15 days of water deficit; D_2), salt (200 mM NaCl; S_1 and 400 mM NaCl; S_2), Cd stress (2 mM $CdCl_2$; Cd_1 and 4 mM $CdCl_2$; Cd_2), and waterlogging (5 days of waterlogging; WL_1 and 15 days of waterlogging; WL_2). Here first dose of each treatment was termed as moderate one and second dose was termed as severe. Plants were exposed to salt and Cd treatments for 15 days. All data were collected from 30-days-old plant. The experiment was held in randomized complete block design with three replications.

2.2 Plant height and biomass

For measuring plant height, three plants were selected from each pot and average height was taken.

From each pot, randomly three plants were uprooted, cleaned to remove soil, and weighed in a balance and then average was calculated to get fresh weight (FW) plant^{-1}. After weighing FW, samples were dried in an electric oven maintaining 80°C for 48 h. Then, the samples were weighed in an electric balance and average was considered as dry weight (DW) plant^{-1}.

2.3 Leaf area

For leaf area measurement, first leaf images were taken by a digital camera and the area was calculated using Image-J software [16].

2.4 SPAD value

From each pot, five leaves were randomly selected and with SPAD meter (atLEAF, FT Green LLC, USA) and atLEAF value was taken. Then it was averaged and SPAD value was measured by the conversion of atLEAF value into SPAD units.

2.5 Leaf relative water content (RWC)

RWC of leaf was measured following the procedure of Barrs and Weatherly [17]. Whole leaf discs were weighed as FW and then dipped into distilled water in Petri dishes and kept in a dark place. After 24 h, excess surface water was removed and leaf discs were weighed again which were considered as turgid weight (TW). Then, after drying at 80°C for 48 h DW was measured. Leaf RWC was calculated using the following formula:

$$\text{RWC}\ (\%) = \frac{\text{FW} - \text{DW}}{\text{TW} - \text{DW}} \times 100.$$

2.6 Stem diameter

Stem diameter of plants was recorded after the duration of stress treatment was completed. Stem diameter was taken by using slide calipers.

2.7 Measurement of lipid peroxidation and hydrogen peroxide content

The lipid peroxidation level was measured in terms of MDA content following the method of Heath and Packer [18]. The leaf samples were extracted by using trichloroacetic acid (TCA) and centrifuged at 11,500 × *g*. The collected supernatant was mixed with thiobarbituric acid reagent. The spectrophotometric absorbance was recorded at 532 nm and corrected at 600 nm.

Following the method of Yu et al. [19], H_2O_2 was assayed where leaf samples were homogenized by using TCA and centrifuged at 11,500 × *g*. Leaf extracts were mixed with potassium phosphate (K-P) buffer (pH 7.0) and potassium iodide (KI). Optical absorption of the supernatant was measured spectrophotometrically at 390 nm to determine the H_2O_2 content.

2.8 Estimation of electrolyte leakage (EL)

EL was calculated following the method of Dionisio-Sese and Tobita [20]. Smaller pieces of leaf were put into falcon tubes containing deionized H_2O and heated at 40°C. After cooling at room temperature, EC_1 was measured using HI-993310 electrical conductivity meter (Hanna, USA). The falcon tubes were again heated at 121°C and after cooling, the final EC_2 was measured. By using the following formula EL was determined:

$$EL = EC_1/EC_2 \times 100.$$

2.9 Leaf extraction for determination of protein and enzyme activity

By following the method of Hasanuzzaman et al. [21], leaf sample was homogenized in an ice-cold extraction buffer containing K-P buffer (pH 7.0), ascorbate (AsA), KCl, β-mercaptoethanol, and glycerol. The mixture was centrifuged at 11,500 × *g* for 15 min and the supernatants were collected and then used for determination of enzyme activity. Throughout the overall procedure, 0–4°C temperature was maintained.

2.10 Protein determination

Protein content from enzyme extraction was estimated spectrophotometrically by using a standard curve of known concentration prepared from bovine serum albumin [22].

2.11 Determination of enzyme activities

Ascorbate peroxidase (APX, EC: 1.11.1.11) activity was assayed according to the method of Nakano and Asada [23], where the reaction reagent contained K-P buffer (pH 7.0), reduced AsA, ethylenediaminetetraacetic acid (EDTA), H_2O_2, and enzyme solution. Decreased absorbance was observed at 290 nm and computed using 2.8 $mM^{-1}\,cm^{-1}$ as the extinction coefficient.

Monodehydroascorbate reductase (MDHAR, EC: 1.6.5.4) activity was estimated following Hossain et al. [24], where the reaction mixture comprised tris-HCl buffer (pH 7.5), AsA, ascorbate oxidase, nicotinamide adenine dinucleotide phosphate (NADPH), and enzyme solution. Absorbance was recorded at 340 nm and 6.2 $mM^{-1}\,cm^{-1}$ was used as the extinction coefficient.

Dehydroascorbate reductase (DHAR, EC: 1.8.5.1) activity was determined following the method of Nakano and Asada [23], where K-P buffer (pH 7.0), reduced glutathione (GSH), dehydroascorbate (DHA), EDTA, and enzyme solution were mixed to make a reaction solution. The activity of DHAR was estimated by observing the absorbance at 265 nm. Extinction coefficient of 14 $mM^{-1}\,cm^{-1}$ was used during the enzyme calculation.

Glutathione reductase (GR, EC: 1.6.4.2) activity was assayed following Hasanuzzaman et al. [21], where the reaction mixture solution comprised K-P buffer (pH 7), oxidized glutathione (GSSG), EDTA, NADPH, and enzyme solution. The decrease in absorbance was recorded at 340 nm and enzyme activity was calculated using 6.2 $mM^{-1}\,cm^{-1}$ as the extinction coefficient.

Glutathione *S*-transferase (GST, EC: 2.5.1.18) activity was estimated according to Nahar et al. [25], where the assay solution comprised tris-HCl buffer (pH 6.5), 1-chloro-2,4-dinitrobenzene (CDNB), GSH, and enzyme solution. The activity was obtained by observing the increase in absorbance at 340 nm and using 9.6 $mM^{-1}\,cm^{-1}$ as the extinction coefficient.

Glutathione peroxidase (GPX, EC: 1.11.1.9) activity was assayed following the method described by Nahar et al. [25], where the reaction solution contained K-P buffer (pH 7), GSH, EDTA, GR, sodium azide (NaN_3), NADPH, H_2O_2, and enzyme solution. The activity was computed by observing the absorbance at 340 nm. Extinction coefficient of 6.62 $mM^{-1}\,cm^{-1}$ was used during the calculation of enzyme activity.

Catalase (CAT, EC: 1.11.1.6) activity was measured by using a reaction mixture containing K-P buffer (pH 7.0), H_2O_2, and enzyme solution. The decrease in absorbance was observed at 240 nm and computed using 39.4 $M^{-1}\,cm^{-1}$ as the extinction coefficient [26].

Glyoxalase I (Gly I, EC: 4.4.1.5) activity was determined using the method described by Hasanuzzaman et al. [27], where the reaction solution contained K-P buffer (pH 7.0), GSH, magnesium sulfate ($MgSO_4$), and methylglyoxal (MG). Increased absorbance was observed at 240 nm using 3.37 mM^{-1} cm^{-1} as the extinction coefficient.

Glyoxalase II (Gly II, EC: 3.1.2.6) activity was measured according to Hasanuzzaman et al. [21], where the assay buffer contained tris-HCl buffer (pH 7.2), 5,5′-dithiobis (2-nitrobenzoic acid) (DTNB), and *S*-D-lactoylglutathione (SLG). The activity was monitored at 412 nm by using an extinction coefficient of 13.6 mM^{-1} cm^{-1}.

2.12 Statistical analysis

Data accumulated from different parameters were subjected to analysis of variance (ANOVA) using the software CoStat v.6.400 [28] and mean separation was compared by Least Significant Difference (LSD) at 5% level of significance. Correlation analysis was done considering 1% level of significance by using SPSS v.27 [29].

3 Results

3.1 Plant height, biomass, and leaf area

Plant height decreased upon exposure to different abiotic stresses (Figure 1a). Plant height decreased by 8 and 28% in moderate and severe doses of salt stress, respectively. However, 13 and 16% reduction in plant height was also observed in mild and severe stresses of drought, respectively. Moderate (8%) and severe (25%) doses of Cd also caused reduction in plant height. In moderate waterlogging stress, plant height reduced by 38%; however, maximum reduction (41%) was observed in severe waterlogging stress.

In this study, a sharp decrease in above ground FW was noticed in both doses of treatments (Figure 1b). During exposure to salt, drought, and Cd stresses, above ground FW decreased by 16, 22, and 20% in moderate level and 35, 30, and 26% in severe level of stress, respectively, over control. Above ground FW reduced by 35 and 38% in WL_1 and WL_2, respectively.

A sharp decrease in above ground DW was noticed in both doses of treatments. Severe level of salt, drought,

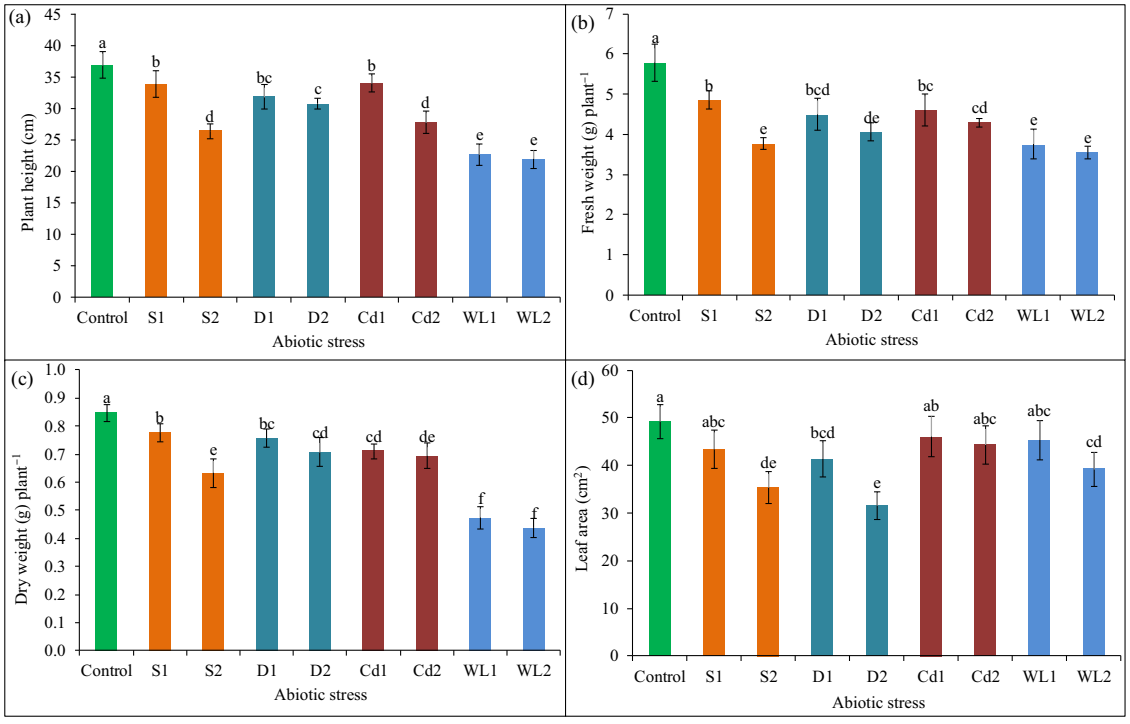

Figure 1: Plant height (a), FW (b), DW (c), and leaf area (d) of *C. olitorius* plants affected by different abiotic stresses. S_1, S_2, D_1, D_2, Cd_1, Cd_2, WL_1, and WL_2 represent 200 mM of NaCl, 400 mM of NaCl, 10 days of water deficit, 15 days of water deficit, 2 mM of $CdCl_2$, 4 mM of $CdCl_2$, 5 days of waterlogging, and 15 days of waterlogging, respectively. Mean value (±SD) was calculated from three replicates for each treatment. Values in a column with different letters are significantly different at $p \leq 0.05$ applying LSD test.

and Cd stresses reduced DW by 26, 16, and 19%, respectively, over control (Figure 1c). Above ground DW reduced by 45 and 48% in WL_1 and WL_2, respectively, and both were statistically similar.

Leaf area showed completely different responses at different abiotic stresses (Figure 1d). Upon exposure to different levels of Cd stress, leaf area showed no sharp changes. Only severe levels of salinity and waterlogging sharply reduced leaf area by 28 and 21%, respectively. However, drought stress reduced leaf area at both levels of stress (16 and 36%).

3.2 SPAD value

Reduction in SPAD value was observed in all abiotic stresses (Figure 2). However, remarkable reduction was observed in WL_2 compared to other stresses. SPAD value decreased by 6 and 9% at short- and long-terms of water deficit condition and by 5, 8, 10, 17, 29, and 31% in S_1, S_2, Cd_1, Cd_2, WL_1, and WL_2, respectively over control.

3.3 Leaf RWC

Exposure to different abiotic stresses resulted in reduction in RWC at any level of treatments (except in WL_1). Both D_1 and D_2 reduced RWC by 16 and 23%, respectively. However, RWC reduced by 16, 11, and 8% in Cd_1, Cd_2, and WL_2, respectively. Drastic reduction was observed in both salt stresses by 23 and 25% (Figure 3).

3.4 Stem diameter

In this study, stem diameter reduced upon exposure to different abiotic stresses (Figure 4). Stem diameter reduced sharply at severe doses of treatments than the moderate ones. Stem diameter decreased by 56, 61, 57, and 58% in severe levels of salt, drought, Cd, and waterlogging stresses, respectively, corresponding to control.

3.5 Oxidative stress indicators

In this study, a sharp increase in MDA content was noticed in all treatments (Figure 5a). MDA content increased by 25, 101, 20 and 24% in moderate level of salt, drought, Cd and waterlogging stresses and 83, 137, 40, and 39% in severe doses of salt, drought, Cd, and waterlogging stresses, respectively, compared to control.

In this experiment, H_2O_2 content increased sharply upon exposure to different abiotic stresses (Figure 5b). Highest H_2O_2 content was noticed in drought stress and it increased with the severity of stress (83 and 101%). In S_1, S_2, Cd_1, and Cd_2, H_2O_2 content increased by 58, 68, 36, and 46%, respectively, corresponding to control. During short-term waterlogged condition, H_2O_2 content increased by 30% which was statistically similar with that of long-term waterlogged condition (40%).

EL remarkably increased in all extent of treatments, except in moderate Cd stress (Figure 5c). In moderate levels of salt, drought, and waterlogging stresses, EL

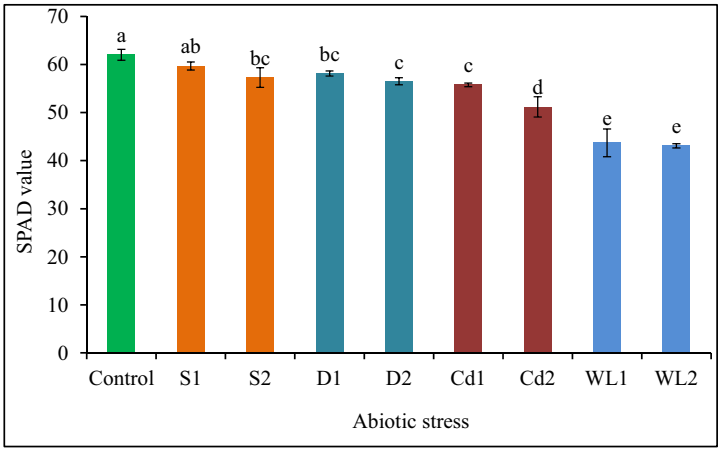

Figure 2: SPAD value of *C. olitorius* plants affected by different abiotic stresses. S_1, S_2, D_1, D_2, Cd_1, Cd_2, WL_1, and WL_2 represent 200 mM of NaCl, 400 mM of NaCl, 10 days of water deficit, 15 days of water deficit, 2 mM of $CdCl_2$, 4 mM of $CdCl_2$, 5 days of waterlogging, and 15 days of waterlogging, respectively. Mean value (±SD) was calculated from three replicates for each treatment. Values in a column with different letters are significantly different at $p \leq 0.05$ applying LSD test.

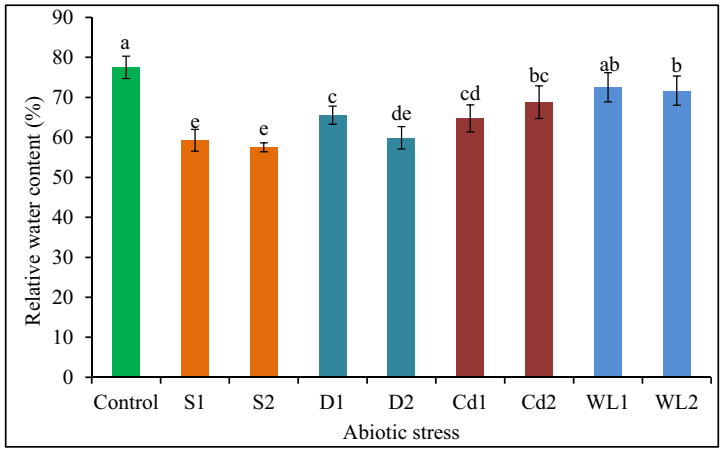

Figure 3: RWC of *C. olitorius* plants affected by different abiotic stresses. S_1, S_2, D_1, D_2, Cd_1, Cd_2, WL_1, and WL_2 represent 200 mM of NaCl, 400 mM of NaCl, 10 days of water deficit, 15 days of water deficit, 2 mM of $CdCl_2$, 4 mM of $CdCl_2$, 5 days of waterlogging, and 15 days of waterlogging, respectively. Mean value (±SD) was calculated from three replicates for each treatment. Values in a column with different letters are significantly different at $p \leq 0.05$ applying LSD test.

increased by 43, 126, and 34% and 153, 54, and 52% in severe doses of salt, Cd, and waterlogging stresses, respectively, corresponding to control. Highest amount of EL was observed in severe drought stress (251%).

3.6 Activities of antioxidant enzymes

Activity of APX remarkably increased in all extent of treatments (Figure 6a). In moderate levels of salt, drought, Cd, and waterlogging stresses, APX activity increased by 59, 87, 27, and 52% and 82, 98, and 80% in severe doses of salt, drought, and Cd stresses, respectively, corresponding to control. However, highest activity was observed in severe waterlogging stress (251%).

A sharp decrease in MDHAR activity was noticed in both doses of treatments (Figure 6b). In moderate and severe salt stresses, MDHAR activity decreased by 30 and 43%, respectively, and 48 and 52% in water deficit stress. In Cd and waterlogged conditions, MDHAR activity decreased in both moderate and severe doses of treatments by 19 and 30% and 20 and 54%, respectively, corresponding to control.

Exposure to different abiotic stresses resulted in decrease in DHAR activity of plant (Figure 6c). In severe levels of salt, drought, Cd and waterlogging stresses, DHAR activity decreased by 31, 32, 20, and 38% and 22,

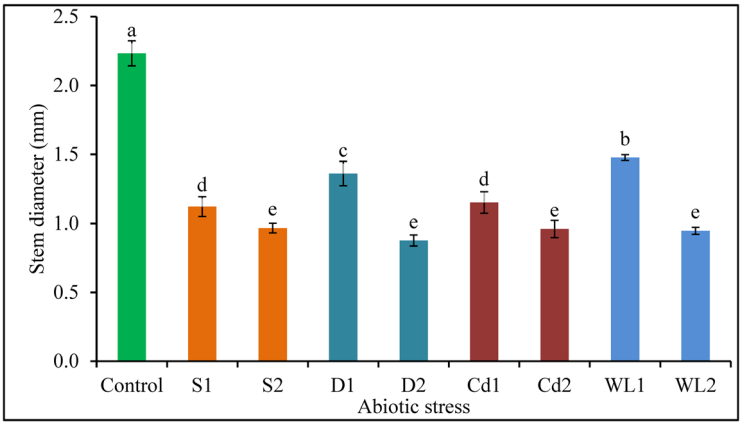

Figure 4: Stem diameter of *C. olitorius* plants affected by different abiotic stresses. S_1, S_2, D_1, D_2, Cd_1, Cd_2, WL_1, and WL_2 represent 200 mM of NaCl, 400 mM of NaCl, 10 days of water deficit, 15 days of water deficit, 2 mM of $CdCl_2$, 4 mM of $CdCl_2$, 5 days of waterlogging, and 15 days of waterlogging, respectively. Mean value (±SD) was calculated from three replicates for each treatment. Values in a column with different letters are significantly different at $p \leq 0.05$ applying LSD test.

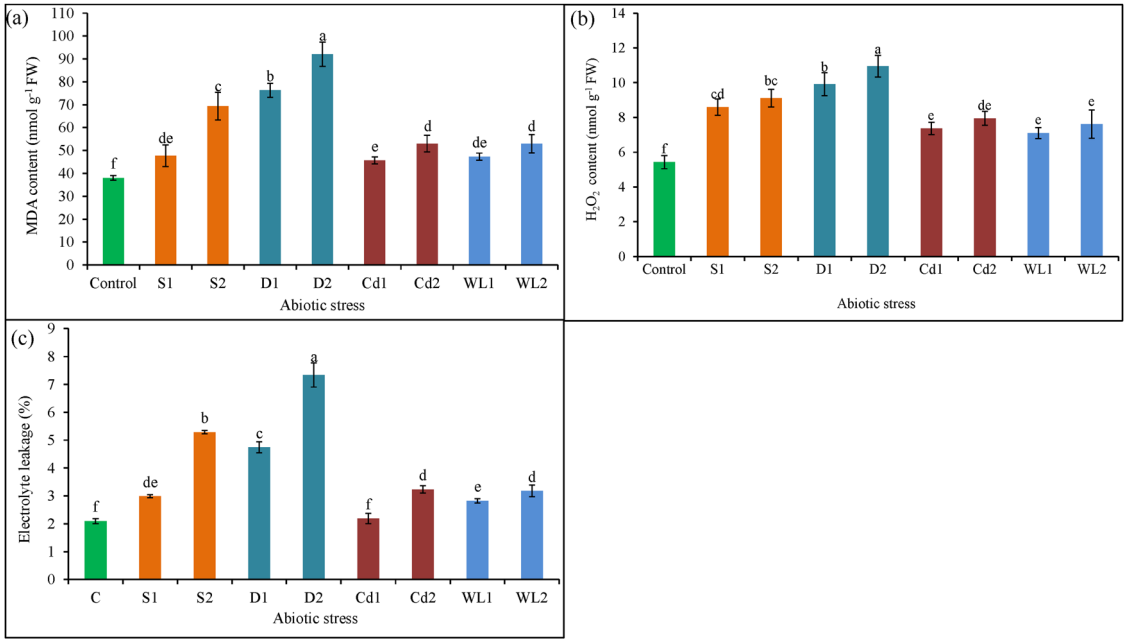

Figure 5: MDA (a), H_2O_2 (b), and EL (c) contents of *C. olitorius* plants affected by different abiotic stresses. S_1, S_2, D_1, D_2, Cd_1, Cd_2, WL_1, and WL_2 represent 200 mM of NaCl, 400 mM of NaCl, 10 days of water deficit, 15 days of water deficit, 2 mM of $CdCl_2$, 4 mM of $CdCl_2$, 5 days of waterlogging, and 15 days of waterlogging, respectively. Mean value (±SD) was calculated from three replicates for each treatment. Values in a column with different letters are significantly different at $p \leq 0.05$ applying LSD test.

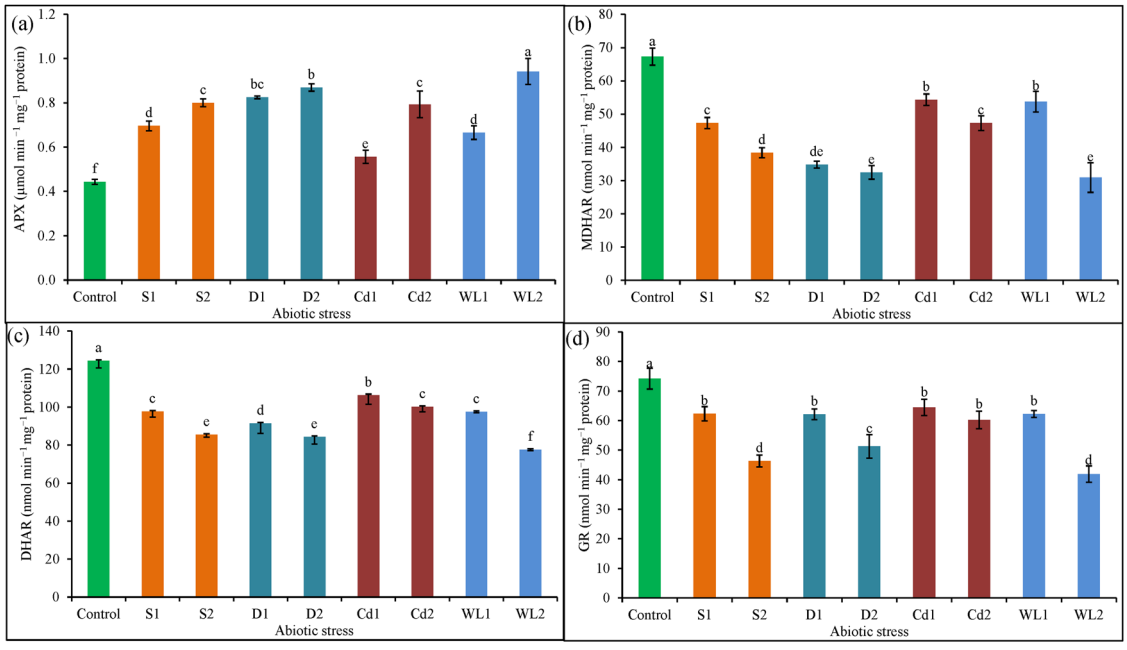

Figure 6: APX (a), MDHAR (b), DHAR (c), and GR (d) activities of *C. olitorius* plants affected by different abiotic stresses. S_1, S_2, D_1, D_2, Cd_1, Cd_2, WL_1, and WL_2 represent 200 mM of NaCl, 400 mM of NaCl, 10 days of water deficit, 15 days of water deficit, 2 mM of $CdCl_2$, 4 mM of $CdCl_2$, 5 days of waterlogging, and 15 days of waterlogging, respectively. Mean value (±SD) was calculated from three replicates for each treatment. Values in a column with different letters are significantly different at $p \leq 0.05$ applying LSD test.

27, 15, and 22% in moderate doses of salt, drought, Cd and waterlogging stresses, respectively, over control.

Exposure to different abiotic stresses resulted in decrease in GR activity of plant (Figure 6d). In moderate

levels of salt, drought, Cd, and waterlogging stresses, GR activity decreased by 16, 16, 13, and 16% which were statistically similar and 38, 31, 19 and 43% in severe doses of salt, drought, Cd, and waterlogging stresses, respectively, over control.

In this study, a sharp decrease in CAT activity was noticed in both doses of treatments (except in Cd_1). In severe Cd stress, CAT activity decreased by 52% (Figure 7a). In moderate and severe salt stresses, CAT activity decreased by 17 and 28%, respectively, over control. In water deficit and waterlogged conditions, CAT activity decreased in both moderate and severe doses of treatments by 19, 53, 31, and 68%, respectively, corresponding to control.

In this study, GPX activity reduced upon exposure to different abiotic stresses (Figure 7b). Activity of GPX reduced sharply at severe doses of treatments than the moderate ones. Highest reduction was observed in WL_2 (60%). GPX activity decreased by 20, 13, 13, and 47% in S_1, D_1, Cd_1, and WL_1 and 20, 27, and 33% in S_2, D_2, and Cd_2, respectively, corresponding to control.

Reduction in GST activity was observed in all abiotic stresses (Figure 7c). However, remarkable reduction was observed in WL_2 (40%) and S_2 (33%) compared to other stresses. Statistically similar reduction (21%) was observed in S_1, D_1, D_2, Cd_1, Cd_2, and WL_1.

3.7 Activities of glyoxalase enzymes

A sharp decrease in Gly I activity was noticed in both doses of treatments (Figure 8a). The highest reduction in Gly I activity was observed in Cd_2 (55%) and long-term waterlogging stress (57%). In moderate salt, water deficit, Cd, and waterlogging stresses, Gly I activity decreased by 20, 16, 24 and 38%, respectively. In severe salt and water deficit conditions, Gly I activity decreased by 24 and 40%, respectively, corresponding to control.

Activity of Gly II remarkably decreased in all extent of treatments (Figure 8b). In moderate levels of salt, drought, Cd, and waterlogging stresses, Gly II activity decreased by 11, 34, 15, and 49% and 25, 50, and 46% in severe doses of salt, drought, and Cd stresses, respectively, corresponding to control. However, highest reduction in activity was observed in long-term waterlogging stress (65%) over control.

3.8 Correlation among the parameters

It was clear from the correlation study (Figure 9) that oxidative stress indicators viz. EL, MDA, and H_2O_2 were

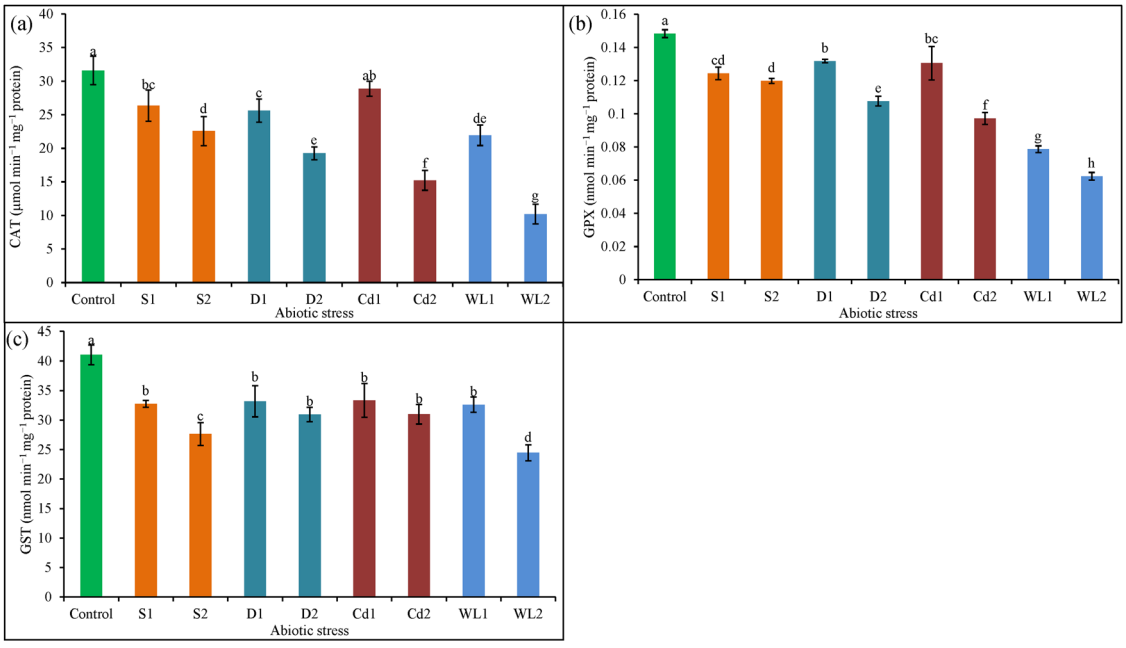

Figure 7: CAT (a), GPX (b), and GST (c) activities of *C. olitorius* plants affected by different abiotic stresses. S_1, S_2, D_1, D_2, Cd_1, Cd_2, WL_1, and WL_2 represent 200 mM of NaCl, 400 mM of NaCl, 10 days of water deficit, 15 days of water deficit, 2 mM of $CdCl_2$, 4 mM of $CdCl_2$, 5 days of waterlogging, and 15 days of waterlogging, respectively. Mean value (±SD) was calculated from three replicates for each treatment. Values in a column with different letters are significantly different at $p \leq 0.05$ applying LSD test.

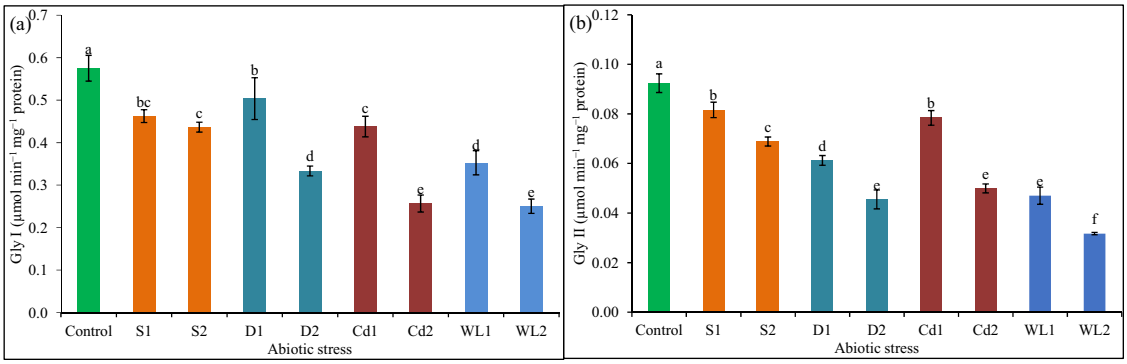

Figure 8: Gly I (a) and Gly II (b) activities of *C. olitorius* plants affected by different abiotic stresses. S_1, S_2, D_1, D_2, Cd_1, Cd_2, WL_1, and WL_2 represent 200 mM of NaCl, 400 mM of NaCl, 10 days of water deficit, 15 days of water deficit, 2 mM of $CdCl_2$, 4 mM of $CdCl_2$, 5 days of waterlogging, and 15 days of waterlogging, respectively. Mean value (±SD) was calculated from three replicates for each treatment. Values in a column with different letters are significantly different at $p \leq 0.05$ applying LSD test.

negatively correlated with plant height, leaf area, FW, DW, SPAD, stem diameter, and all the antioxidant enzymes. Most of the parameters were highly affected by the treatments except leaf area and RWC.

4 Discussion

In this experiment, plant growth decreased at different abiotic stresses in a dose-dependent manner at any ages of plant growth (Figure 1). After imposing abiotic stress on plant, growth arrest is the first response of plant which causes metabolic reduction and gradually reduces shoot growth [30]. In the present study, salinity-induced osmotic stress causes reduction in plant biomass (FW and DW). Naik et al. [10] also observed reduction in FW and DW at 100 and 160 mM of NaCl-induced salt stress in different varieties of *C. olitorius* plant. Due to water unavailability in drought stress, plants' metabolism and physiological processes are greatly hampered. As a result, net photosynthesis is reduced and growth is stunted ultimately leading toward reduction in growth parameters [31]. At constant drought (8-10% soil moisture) condition, plant height of *C. olitorius* cultivar O-4 decreased by 50% [9]. Leaf area is an indication of plant growth which was reduced by 2- and 4-folds in *C. olitorius* at 70 and 40% field capacity (FC), respectively [32]. In several studies, Saleem et al. [33,34] observed the reduction in leaf area of *C. capsularis* plant at different levels of Cu stress. Waterlogging causes nutrient deficiencies in plant which disrupts physiological process and reduces the biomass of plant [35]. Ghorai et al. [36] found 41% reduction in plant height of *C. olitorius* at 30 cm water regime. *C. olitorius* plants were unable to withstand waterlogged condition at early growth stages and caused drastic growth reduction [37].

In our present study, SPAD value decreased due to different abiotic stresses in a dose-dependent manner at any ages of plant growth (Figure 2, drought stress damaged photosynthetic pigments due to oxidation of pigments and reduced photosynthesis rate). Under salt stress, Na^+ and Cl^- ions concentrations increase in cell which inhibit net photosynthesis rate [38]. In *C. olitorius*, Bhuyan et al. [39] found 13% reduction in SPAD value under 200 mM of NaCl-induced stress. At 40% FC, total chlorophyll (Chl) content of *C. olitorius* reduced by 59% [32]. Similar results were found by Hasanuzzaman et al. [21], where at polyethylene glycol (PEG)-induced drought stress, SPAD value of *Brassica* species reduced by 14–27%. Cd stress reduced water use efficiency of plant and decreased photosynthesis rate and stomatal conductance [40]. Saleem et al. [34] found reduction in total Chl content in *C. capsularis* plant with the increase in the level of Cu stress. Leaf yellowing occurs due to waterlogging stress which reduced photosynthesis rate and Chl content [41].

In this experiment, RWC was decreased due to exposure to different abiotic stresses in a dose-dependent manner at any ages of plant growth (Figure 3). Higher salt concentration creates osmotic stress in plants and ultimately leads toward low water potential and reduced RWC of *Corchorus* spp. at 100 and 200 mM of NaCl-induced salt stress [42]. Drought stress causes unavailability of water and diversely affects plants' physiological process and metabolism which reduced water content in leaf [43]. Yakoub et al. [32] recorded 53% of reduction in RWC in *C. olitorius* plant at 40% moisture condition. Higher concentration of metals/metalloids negatively affected plants morphophysiology, which reduces plants' water content, imbibition, transpiration rate, osmotic

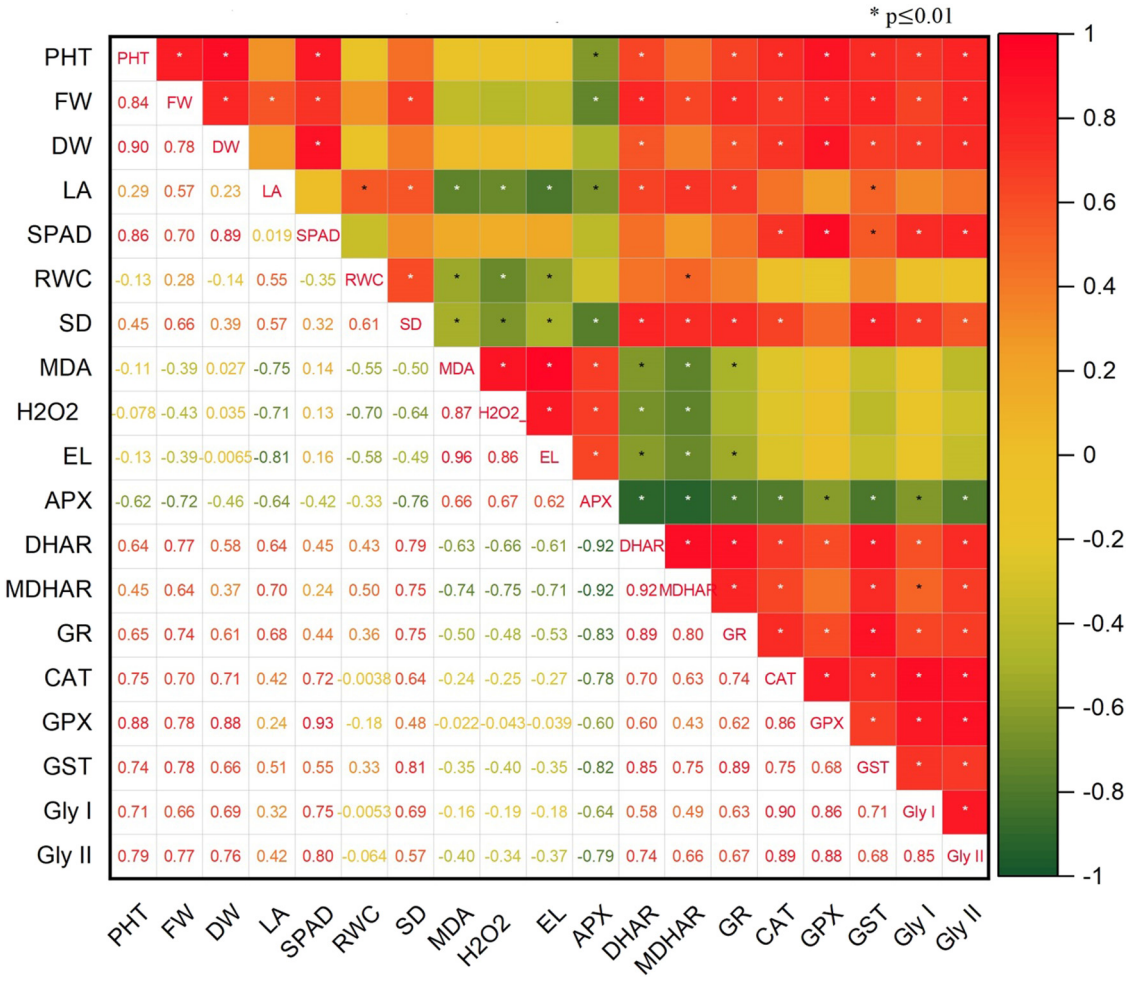

Figure 9: Correlation analysis of different studied parameters (PHT – Plant height; LA – Leaf area; FW – Fresh weight; DW – Dry weight; SD – Stem diameter; SPAD; RWC – Relative water content; EL – Electrolyte leakage; MDA – Malondialdehyde; H_2O_2 – Hydrogen peroxide content; APX – Ascorbate peroxidase; CAT – Catalase activity; GPX – Glutathione peroxidase; GST – Glutathione *S*-transferase; DHAR – Dehydroascorbate reductase; MDHAR – Monodehydroascorbate reductase; GR – Glutathione reductase; Gly I – Glyoxalase I; Gly II – Glyoxalase II).

pressure, and ultimately RWC. Memari-Tabrizi et al. [44] noticed reduction in RWC in *Satureja hortensis* at 20 mg kg^{-1} of Cd contaminated soil. Due to hypoxic or anoxic condition, plant faces unavailability of water in spite of excess availability of water in flooded condition. In *Sesamum indicum* plants, Anee et al. [45] observed 75% reduction in RWC after 8 days of waterlogging.

In this experiment, stem diameter decreased upon exposure to different abiotic stresses in dose-dependent manner (Figure 4). Salt stress stunted plant growth, specially shoot growth. With the decrease in shoot growth, reduction in stem diameter was also observed. This growth reduction was proportionately related to the increase in Na content [46]. At water deficit condition, main stem growth decreases and causes a sharp decrease in stem diameter of *Helianthus annuus* [47]. Visual symptoms of Cd stress were first observed in upper part of the plants. In *C. capsularis*, Parveen et al. [48] noticed reduction in stem diameter at different level of Cu stress (50 and 100 µM of $CuSO_4$). Waterlogging stress reduced fiber yield and marketable grade of jute by reducing stem diameter [36].

In the present study, MDA and H_2O_2 content increased at different abiotic stresses in a dose-dependent manner at any ages of plant (Figure 5a and b). Plants under salt stress are affected by osmotic stress, nutritional deficiency, ion toxicity, etc., resulting in excessive production of ROS [49]. Ma et al. [11] observed increasing trend in MDA with the increase in salinity in both *C. capsularis* and *C. olitorius* plants. Drought initiates stomatal closure, reduces CO_2 assimilation, and impairs light production which cause excessive production of ROS [50]. Chowdhury and Choudhuri [51] observed increase in H_2O_2 content in *C. capsularis*

plant upon exposure to water deficit condition. At 60% FC condition, MDA content of *Solanum lycopersicum* also increased by 83% [52]. Toxic metal/metalloids produced excessive amount of ROS which causes chloroplastic damage and interfere with mitochondrial activity. Metal stress increases lipid peroxidation and creates membrane denaturation in plants, due to which H_2O_2 content increased in *C. capsularis* plant with the increase in the level of Cu stress [53]. Due to hypoxic and anoxic conditions, waterlogged plants produced toxic compounds which generate excessive ROS and increase lipid peroxidation and H_2O_2 content [54]. Anee et al. [45] and Zhang et al. [35] observed reduction in MDA and H_2O_2 in *S. indicum* and *Sorghum bicolor*, respectively, at different durations of waterlogging.

Ion-specific salt injury occurred first at plasma membrane which caused increase in EL in plants [55]. In this experiment, EL increased at different abiotic stresses in a dose-dependent manner (Figure 5c). With the increase in salt stress, EL in root and leaves of *Lactuca sativa* increased proportionately [56]. Similarly, the increased EL indicates the damage of plasma membrane caused by drought stress. In *Vicia faba*, EL increased positively with the increase in drought stress which caused severe membrane damage and efflux of K^+ [57]. Cd toxicity caused membrane damage in *Nicotiana tabacum* plant and increased EL in a dose-dependent manner which is positively correlated with MDA [58]. Similar results were also observed in *C. capsularis* at different levels of Cu stress (100, 200, 300, and 400 mg kg^{-1}) [59]. The degree of membrane integrity was assessed by the EL in *Zea mays* plants where 48% increase in EL was noticed at 120 h of flooding [60].

Antioxidant enzymes help to reduce excess accumulation of ROS production in stress condition [61]. The activities of APX, DHAR, MDHAR, and GR collaborate with AsA and GSH and help to upregulate AsA–GSH pool to diminish ROS [62]. They reduce H_2O_2 content and help to maintain redox homeostasis [50]. In our present study, APX activity increased and MDHAR, DHAR, and GR activities decreased in a dose-dependent manner (Figure 6). Similar results were also recorded in *S. lycopersicum* at 150 mM NaCl-induced salt stress [63]. Saad-Allah and Nessem [64] observed reduction in GR activity of *C. olitorius* plant under salt-stressed condition. Hasanuzzaman et al. [21] also recorded enhanced APX activity and diminished MDHAR, DHAR, and GR activities in *B. napus* at 20% PEG-induced drought condition. Saleem et al. [59] observed increased activity of APX in *C. capsularis* seedlings at different levels of Cu stress. Due to the overproduction of ROS, increased APX activity was recorded in *Z. mays* at 21 h waterlogging condition [65] and demolished activity of GR and MDHAR were recorded in *G. hirsutum* plant after 6 days of waterlogging [66].

Among all the antioxidant enzymes, CAT is known as a first-line of defense, which act as a detoxifying agent and convert H_2O_2 to H_2O, to maintain the ROS equilibrium [5]. In this experiment, H_2O_2 content increased with the severity of abiotic stresses which cause decrease in CAT activity (Figure 7a). Ma et al. [11] found higher CAT activity in salt resistant *Corchorus* spp. variety (cv. Huang No.1) compared to the salt susceptible (cv. Menguyan) one. Chowdhury and Choudhuri [51] and Das et al. [67] also recorded decrease in CAT activity in *C. capsularis* with the increase in H_2O_2 content at water deficit condition. Metal resistant variety reduces lipid peroxidation by increasing the CAT activity in *Hibiscus cannabinus* plant [68]. In *Z. mays*, waterlogging tolerant variety shows higher CAT activity compared to the resistant one which indicate their ability to reduce excess ROS production [69]. Cell toxic substances are removed by GPX and GST with the help of GSH to reduce cell damage [5]. Along with H_2O_2 detoxification, GST also has a xenobiotic property which helps to reduce the excess accumulation of ROS [50]. In our study, both GST and GPX activities reduced during the exposure to different abiotic stresses (Figure 7b and c). These findings supported the results of Rahman et al. [70] and Mohsin et al. [71] at Cd-stressed *Oryza sativa* and salt-stressed *Triticum aestivum*, respectively.

Glyoxalase enzymes (viz. Gly I and Gly II) actively participate in detoxifying MG by converting α-ketoaldehydes into hydroxyacids and reduced cell damage in plants [72,73]. In this experiment, activities of Gly I and Gly II (Figure 8) reduced with the extent of abiotic stress. Mohsin et al. [71] also observed reduction in Gly I and Gly II in *T. aestivum* which are negatively related with MG content under salt stress.

In our study, we observed negative correlation of oxidative stress indicators with most of the parameters including antioxidant enzymes. This negative correlation of oxidative stress and antioxidant enzymes indicates the loss of equilibrium and excess generation of ROS under different abiotic stresses. Similar results were demonstrated by Anee et al. [45] at waterlogged condition in *S. indicum* where they recorded negative effect of oxidative stress indicators with antioxidant enzymes.

5 Conclusion

From the findings of this study, it was observed that *C. olitorius* responded differently under different abiotic stresses and these reductions occurred in a dose- or duration-

dependent manner. Growth parameters and SPAD values were highly sensitive to waterlogging followed by drought. At severe waterlogging stress, the upregulation of antioxidant enzymes activities was more crucial compared to any stress. However, severe oxidative damage and ion leakage were recorded in drought stress compared to other stresses. Due to the continuous climate change and stressful environment, nowadays jute plants face many kinds of environmental stress. However, very less work has been conducted regarding the responses of *C. olitorius* under different abiotic stresses. Further studies are required to explore the physiological, biochemical, and genetic responses of *C. olitorius* plants under different abiotic stresses which will be helpful for understanding the tolerance mechanism. This experiment can be a promising phenomenon to create a further scope of investigation at molecular level to tailor stress tolerance parameters of *C. olitorius* and eventually tolerant varieties.

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