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Effect of Selenium on Growth, Physio-Biochemical and Yield Traits of Lettuce under Limited Water Regimes

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Abstract: Climate change has become one of the most complicated challenges of the twenty-first century. Water scarcity is a significant threat to food security, and climate change has adversely affected the likelihood of extreme events such as drought. Selenium (Se) has been reported to mitigate abiotic stress effects, such as drought, on various plant species. The purpose of the current study was to observe the effects of foliar-applied Se to minimize the detrimental effects of water-deficient conditions. Therefore, this study was designed to evaluate the exogenous application of Se at various levels (0, 3, 6 and 9 mg L^{-1}) on the growth, physio-biochemical attributes and antioxidant defense system of lettuce plants growing under an irrigation water deficit from 85 ± 5% (control) to 35 ± 5% (drought stress). The results revealed that increasing water deficit stress linearly reduced plant growth and biomass by reducing relative water content (19.49%) and chlorophyll contents (23.95%) through increased electrolyte leakage (20.67%). However, foliar-applied Se significantly increased fresh and dry biomass under control and water-stressed conditions. Under drought stress, Se supply increased free proline content and the activities of SOD, POD and CAT in leaf tissues. The exogenous application of Se partly alleviated the effects of drought on lettuce by the upregulation of the antioxidant system and leaf soluble sugars and a simultaneous decrease in electrolyte leakage. This study further suggests that the upregulation of antioxidants and osmoprotectants is positively associated with the drought tolerance of lettuce. In conclusion, the exogenous application of Se (6 mg L^{-1}) has more potential to improve lettuce growth, physiological attributes and modulation of enzymatic antioxidant potential, which can be recommended for use to maximize lettuce productivity and quality in a dry environment. This research provides a promising, technically feasible strategy for mitigating drought stress in order to achieve the Sustainable Development Goals (SDGs) of good health and zero hunger.

Keywords: antioxidants potential; drought; foliar; growth; lettuce; osmoprotectants; SDGs

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Citation: Tufail, B.; Ashraf, K.; Abbasi, A.; Ali, H.M.; Sultan, K.; Munir, T.; Khan, M.T.; uz Zaman, Q. Effect of Selenium on Growth, Physio-Biochemical and Yield Traits of Lettuce under Limited Water Regimes. *Sustainability* **2023**, *15*, 6804. https://doi.org/10.3390/su15086804

Academic Editor: M. Iqbal R. Khan

Received: 16 February 2023
Revised: 26 March 2023
Accepted: 15 April 2023
Published: 18 April 2023

1. Introduction

Globally, and notably, in developing nations of South Asia, such as Pakistan, water shortage as a result of climatic change has become a significant challenge to sustainable crop production [1]. Droughts in the agriculture sector pose a substantial threat to crop failure and the resulting food shortages [2–4]. The physiological and biochemical activities of plants, including the photosynthetic rate, osmotic potential, turgor pressure and severe membrane damage, are negatively affected by water stress [5]. It is feasible to maximize agricultural productivity by assessing and minimizing drought's impacts on crops [6].

Due to its high mineral content, improved cholesterol metabolism and antioxidant characteristics, lettuce (*Lactuca sativa*) is one of the most popular vegetables. It has a cultivation area of 1.3 million hectares and a global production of 29 million tons, making it one of the most widely cultivated green vegetables [7]. Traditional cultivation techniques include hydroponic systems, greenhouses and nurseries, but open-field agriculture is also prevalent [8,9]. Both the plant genotype and growth conditions, such as temperature, irrigation, nutrient solution and light quality, can impact lettuce quality, notably in terms of phytochemistry and visual appearance. In addition, effective irrigation management is intimately linked to future production and the availability of healthy soil, which, in turn, affects the yield of horticulture products [10–12]. Therefore, timely drought mitigation strategies are required to safeguard food production in the face of a changing climate.

A recent study suggests that selenium could be a viable mitigating approach [13]. Although it is not essential for plant growth, it is beneficial for plant development [14]. In addition, it increases the photosynthetic capacity, maximum quantum yield of photosystems and photochemical quenching of a variety of plant species [15]. This element may also protect plants from oxidative stress by activating ROS-scavenging pathways during drought stress [16]. Selenium has multiple positive benefits and promotes growth at low concentrations [17]. Numerous researchers have reported that selenium induces drought resistance in plants by limiting water evaporation [18], promoting the synthesis of carotenoids and chlorophyll [19,20] and improving proline accumulation [13]. Selenium supplementation increases drought-induced defense responses in soybeans by enhancing proline accumulation, superoxide dismutase, catalase and glutathione reductase activities, as well as the accumulation of non-enzymatic antioxidants (ascorbate and glutathione). The significance of selenium in increasing the photosynthetic capacity of drought-stressed potatoes has been demonstrated by research on the effect of selenium on drought stress [21]. In soybeans, Galic et al. [22] showed that selenium mitigates drought stress effects by limiting lipid peroxidation and improving osmolyte concentration. Selenium enhances the antioxidative capacity of drought-stressed grapeseed, resulting in low ROS accumulation and lipid peroxidation [23].

The bioavailability of soil-applied Se is lower than that of foliar-applied due to some natural processes such as the immobilization of Fe-Mn oxide [24], redox reactions [25] and losses due to leaching [26]. Therefore, soil application of Se fertilizer is considered disadvantageous due to the lower bioavailability. Foliar- or soil-applied Se can improve the growth and yield of plants; however, foliar-applied Se is more effective than soil applications [13]. Therefore, it becomes necessary to find out some economical and eco-friendly approaches to limit the negative effects of drought stress in lettuce. Based on a literature review, it was found that no study has been conducted yet to investigate the effectiveness of foliar-applied Se at ideal concentrations for lettuce under drought stress conditions. So, the present study is carried out to investigate the protective role of foliage-applied Se in mitigating the adverse effects of an irrigation water deficit (drought stress) by improving the growth characteristics, physiological and biochemical attributes and activity of antioxidant defense system components in lettuce. In addition, this investigation also assesses potential improvements in plant growth, yield and yield quality under drought stress through Se application.

2. Materials and Methods

2.1. Research Location, Experimental Design and Treatments

A pot experiment was carried out in a greenhouse at the Environmental Science Department, The University of Lahore (lat: 31.3881° N and long: 74.2413° E), Pakistan. Experimental treatments consisted of mainly two factors: drought stress D_1 = control (85% ± 5% field capacity) and D_2 = drought stress (35 ± 5% field capacity), and foliar-applied selenium levels, 0, 3, 6 and 9 mg L^{-1}), employing a completely randomized design (CRD) under a factorial arrangement (every replication consisted of three pots per treatment). Total number of pots were (2 × 4 × 3 = 24).

2.2. Experiment Setup and Maintenance

Clay loam soil with pH, 8.05; EC, 1.31 dSm^{-1}; available N, 0.036%; available phosphorus, 26.3 ppm; exchangeable potassium, 315 ppm; and organic matter, 0.92% was used in this experiment to fill the pots (25 top diameter and 23 cm height) with 5 kg of soil. The seeds were decontaminated with 0.1% (*w*/*v*) sodium dodecyl solution and then thoroughly washed using sterilized deionized water. Eight seeds were sown in each pot, and thinning was carried out to maintain five plants when shoots were about 5 cm tall, leaving only the most viable shoots after 15 days of germination. Tap water was used as source of irrigation at field capacity level on a daily basis. Hoagland's solution (50%) was used as a source of nutrients and applied at 500 mL per week per pot. After an acclimatization period of 15 days, drought treatments were applied. Drought stress was maintained through field capacity at desired level, and the field capacity (FC) was calculated by using the equation: FC (%) = water added − water leached. However, during the experiment, pots were weighed at the time of irrigation to maintain the desired soil water level (35% FC) by adding an appropriate amount of water. In each replicate pot, water losses were compensated by applying a measured amount of water to prevail the required field capacity. For each treatment, soil moisture contents were measured on a daily basis by using a soil moisture meter (TZS-W). After 10 days of complete drought stress, foliar application of Se (0, 3, 6 and 9 mg L^{-1}) was conducted using sodium selenite (Na_2SeO_3) as the Se source. Two sprays were used with a 10-day interval, using 500 mL of solution as per treatment. After 15 days of foliar application treatment, data for morphological, biochemical and physiological attributes were recorded.

2.3. Measurement of Growth and Biomass Attributes

Two plants from each replication were collected, and their roots and shoots were separated for the measurements of growth variables. The number of leaves was counted antecedent to the division of plants into shoots and roots. A scale was used to measure the height of the plant as well as the length and width of the leaf. The leaf area was determined by multiplying the leaf length by its width. The fresh weight of the root and leaves was then determined using an analytical balance. To estimate the dry weight of the roots and leaves discreetly, they were oven-dried at 70 °C for 48 h.

2.4. Physio-Biochemical Attributes

To test the electrolyte leakage (EL) level, a small piece of leaf was dipped in purified deionized water. The sample's first EL measurement was obtained following a 2 h incubation at 32 °C, and its second EL reading was obtained following a 20 min incubation at 121 °C. To calculate the EL level of samples, the following formula was used: EL = (EC1/EC2) × 100. Leaf samples (5) were crushed in a test tube with 85% acetone (*v*/*v*) for 24 h and were placed in dark conditions for pigment extraction. After centrifugation for 10 min at 4000× *g* at 4 °C, the absorbance was calculated at 470, 647 and 664.5 nm using a spectrophotometer (Halo DB-20/DB-20S, Barnoldswick, UK), the value in the supernatant was measured and then, according to Lichtenthaler [27] method, the contents of chlorophyll a, b and carotenoids were determined. The total chlorophyll concentrations were measured by the addition of chlorophyll a and b. All the photosynthetic attributes were measured from uppermost leaves with a portable photosynthesis system (infra-red gas analyzer) between 9:00 am and 12:00 pm on a sunny day.

2.5. Enzymatic Antioxidants Activities and Water-Related Attributes

The supernatant extracted from 1 g of lettuce leaves with 50 mM phosphate buffer was centrifuged (~15,000× *g* for 10 min) for determination of enzyme activity. By following the procedure reported by Velikova et al. [28], peroxidase (POD) activity was determined.

Catalase activity (CAT) and superoxide dismutase activity (SOD) were determined according to Aebi [29] and Beauchamp and Fridovich [30] protocols. The method of Turner and Kramer [31] was employed for RWC measurement, and the following formula was used for the calculation: RWC = [(FW − DW)/(TW − DW)] × 100, where FW—fresh weight; TW—turgid weight; DW—dry weight.

2.6. Osmolyte Attributes

A fresh leaf sample (0.5 g) was collected and ground with a buffer (pH value ~7.2) with protease inhibitors of 1 μM, along with saline phosphate buffer. In 1 L of deionized water, the dissolution of 1.37 mM NaCl, 2 mM KH_2PO_4, 2.7 mM KCl and 10 mM Na_2HPO_4 was carried out for the preparation of the saline buffer. By adding HCl to this solution, the pH of the buffer was adjusted. After that, the solution was autoclaved and centrifuged for 5 min for the separation of the supernatant. Proline contents were determined by following the protocols of Maehly and Chance [32], while soluble sugars and soluble proteins were determined by a method defined by Giannakoula et al. [33] and Bradford assay [34], respectively.

2.7. Statistical Analysis

Collected data was tested using Fisher's Analysis of Variance (ANOVA) technique. The highest significant difference (HSD) test (5% probability level) was applied for comparison of means. Regression and correlation analyses were computed by using Minitab-19 statistical software. All statistical computations were performed with Statistix software, version 10 (Analytical Software, Tallahassee, FL, USA), and for the graphical work, Microsoft Excel (2013 version) was employed in this study.

3. Results

3.1. Growth Attributes

Different rates of selenium and drought stress significantly affected ($p \leq 0.01$) the growth attributes of the lettuce plants. Drought stress decreased the root length (28.12%), shoot length (22.06%), number of leaves (34.81%) and head weight (17.35%), as compared to the control. Less variation in growth attributes was found among the foliage-applied selenium treatments, with a significant increase in drought stress treatment only when compared to the control. In terms of growth characteristics under drought stress, the decreasing pattern was control conditions > drought conditions, and for the selenium treatments, 6 mg/L > 9 mg/L > 3 mg/L > 0 mg/L (Figure 1).

3.2. Fresh and Dry Biomass

The fresh and dry biomass of lettuce plants was significantly affected by various levels of selenium treatments, drought stress and their interaction. Drought stress reduced root fresh weight (19.23%), shoot fresh weight (21.28%), plant fresh weight (21.09%), root dry weight (26.15%) and shoot dry weight (32.82%) in comparison with the control. Maximum root fresh weight (6.70 and 5.90 g), shoot fresh weight (67.08 and 58.36 g), plant fresh weight (73.78 and 64.26 g), root dry weight (3.94 and 3.04 g) and shoot dry weight (11.11 and 7.83 g) were observed under control conditions (non-drought) and drought conditions, respectively, where the foliar application of selenium at a rate of 6 mg/L was performed on lettuce plants (Figure 2).

3.3. Biochemical and Water-Related Attributes

Drought-induced stress negatively impacted the biochemical and water-related characteristics of the lettuce plants; however, the foliar application of selenium significantly ($p \leq 0.01$) improved the biochemical and water-related attributes of lettuce plants. Drought stress decreased chlorophyll a (21.80%), chlorophyll b (27.58%), total chlorophyll (23.95%), carotenoid (20.54%) and relative water (19.49%) contents and increased electrolyte leakage (20.67%), as compared to the control. The foliar application of selenium at 6 mg/L decreased electrolyte leakage and improved the water status and other biochemical attributes of lettuce plants under drought stress (Figure 3).

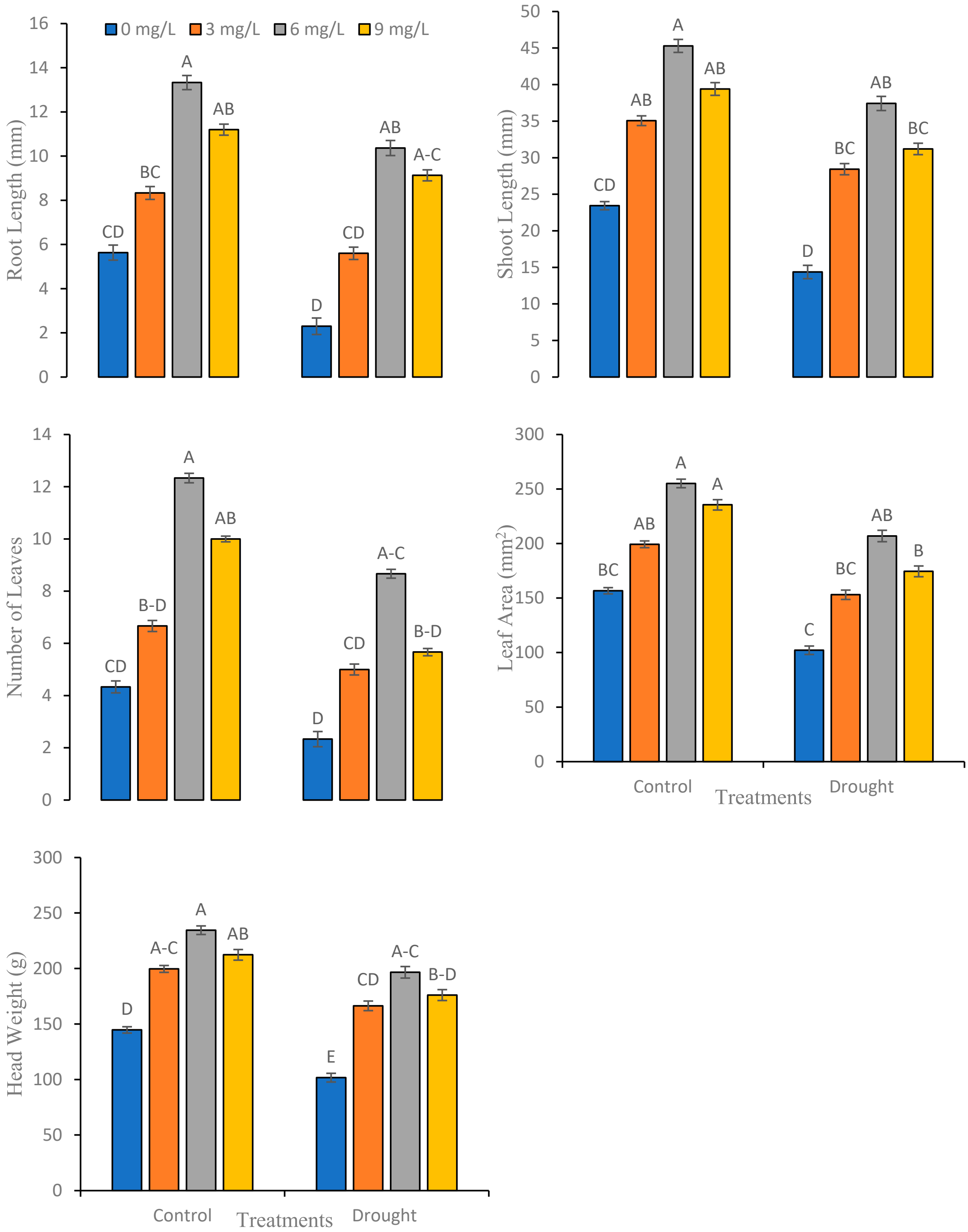

Figure 1. Growth and yield parameters of lettuce treated with varying concentrations of foliar selenium (0, 3, 6 and 9 mg L^{-1}) under normal (85% $\pm$ 5%) and limited water regime circumstances (35% $\pm$ 5%). The uppercase letters in the bars denote significant differences between treatment means at $p \leq 0.05$ (Tukey's HSD); the values represent the means with standard deviation (SD) and were replicated three times.

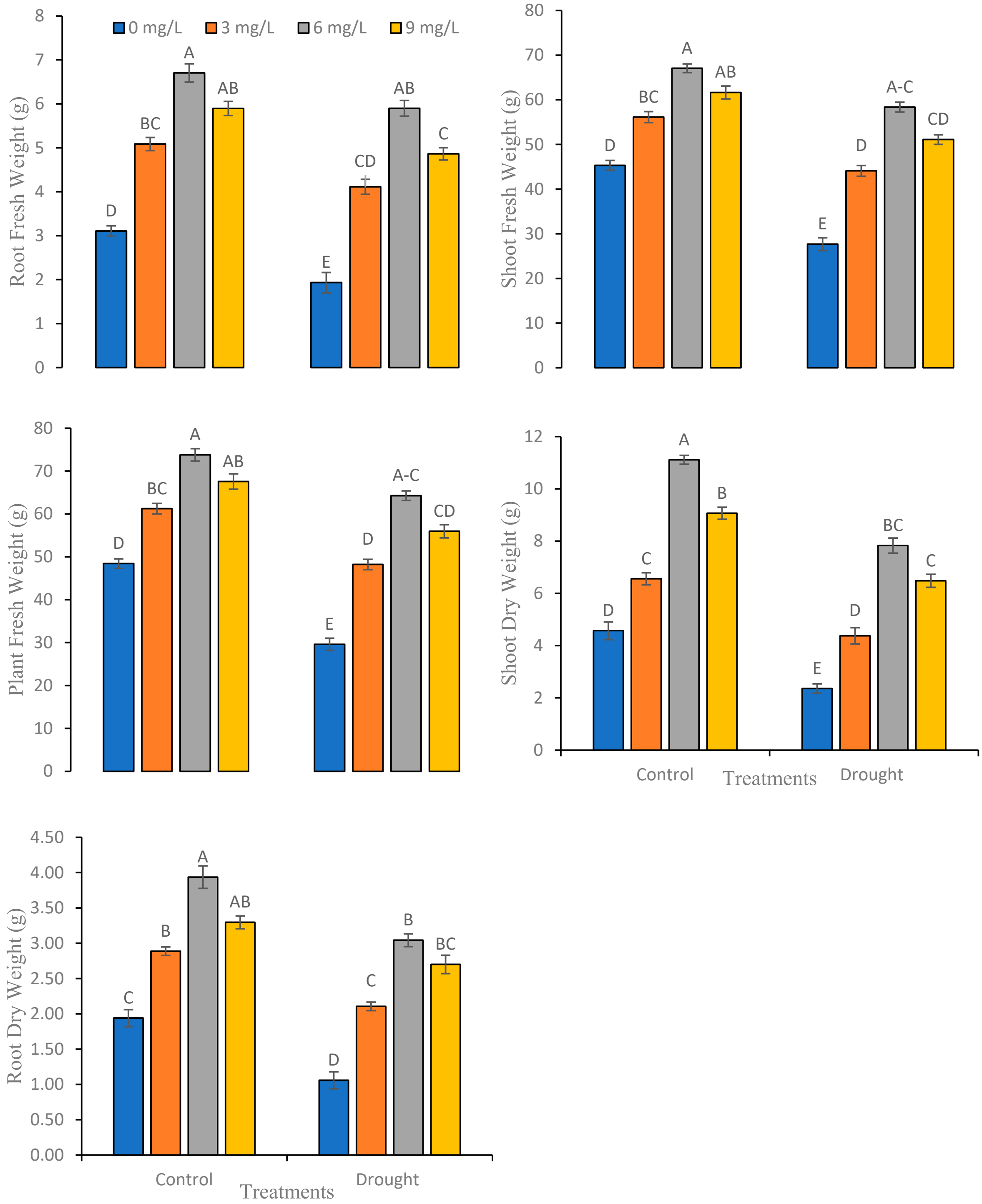

Figure 2. Biomass attributes (fresh and dry) parameters of lettuce treated with varying concentrations of foliar selenium (0, 3, 6 and 9 mg L^{-1}) under normal (85% $\pm$ 5%) and limited water regime circumstances (35% $\pm$ 5%). The uppercase letters in the bars denote significant differences between treatment means at $p \leq 0.05$ (Tukey's HSD); the values represent the means with standard deviation (SD) and were replicated three times.

3.4. Physiological Attributes

Drought stress decreased the photosynthetic rate (34.83%), transpiration rate (26.70%) and stomatal conductance (25.00%), as compared to the control. The maximum physiological values were observed when the foliar application of selenium at a rate of 6 mg/L was applied to lettuce plants. While the minimum photosynthetic rate (5.63 and 2.74 µmol CO_2 m^{-2} s^{-1}), transpiration rate (4.29 and 2.11 mol H_2O m^{-2} s^{-1}) and stomatal conductance (0.42 and 0.24 mol H_2O m^{-2} s^{-1}) were observed under control conditions (non-drought) and drought conditions, respectively, where the foliar application of distilled water (selenium = 0 mg/L) was performed on lettuce plants (Figure 4).

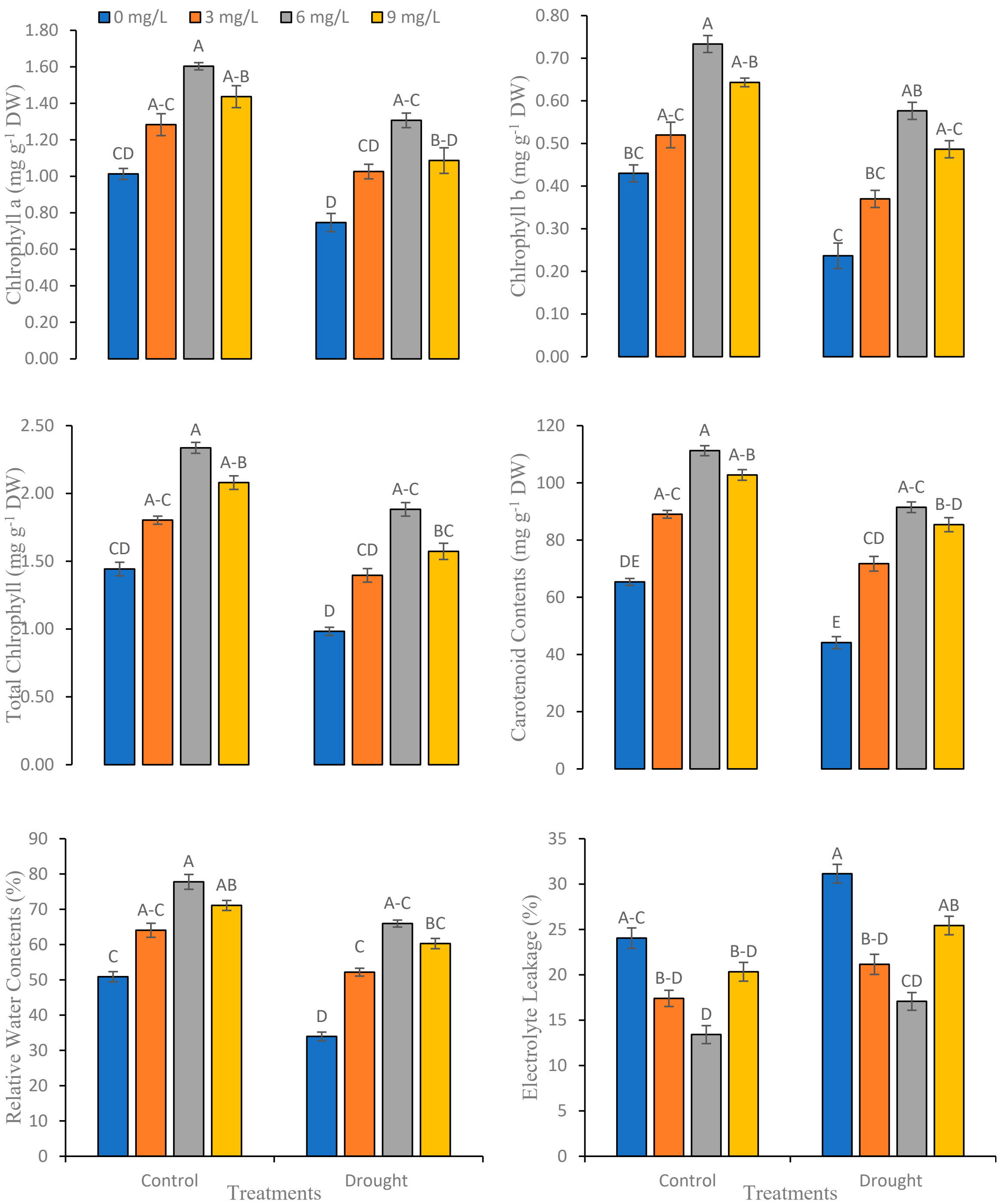

Figure 3. Biochemical parameters of lettuce treated with varying concentrations of foliar selenium (0, 3, 6 and 9 mg L^{-1}) under normal (85% ± 5%) and limited water regime circumstances (35% ± 5%). The uppercase letters in the bars denote significant differences between treatment means at $p \leq 0.05$ (Tukey's HSD); the values represent the means with standard deviation (SD) and were replicated three times.

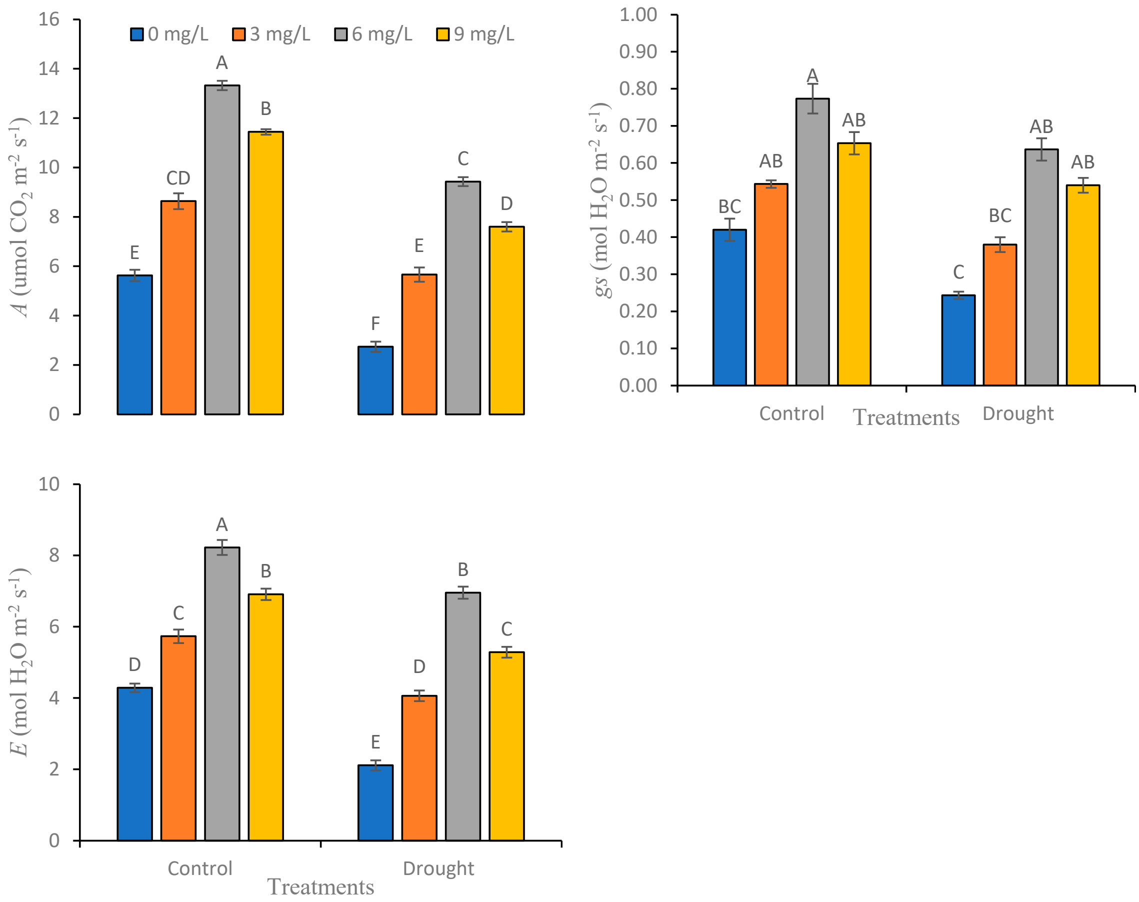

Figure 4. Photosynthetic parameters of lettuce treated with varying concentrations of foliar selenium (0, 3, 6 and 9 mg L^{-1}) under normal (85% ± 5%) and limited water regime circumstances (35% ± 5%). The uppercase letters in the bars denote significant differences between treatment means at $p \leq 0.05$ (Tukey's HSD); the values represent the means with standard deviation (SD) and were replicated three times.

3.5. Enzymatic Antioxidant Activity and Lipid Peroxidation Attributes

The foliar application of selenium treatments under drought stress affected the activity of enzymatic antioxidants of lettuce plants. Limited water stress marked an enhancement in the SOD, POD and CAT activities. Less variation in antioxidant enzyme attributes was found among the foliage-applied treatments, with a significant increase in drought stress treatment only when compared to the control. An observed decreasing pattern, in terms of the activities of antioxidant enzymes, for drought stress was drought conditions > control conditions, and for the selenium treatments, 0 mg/L > 9 mg/L > 3 mg/L > 6 mg/L (Figure 5).

3.6. Osmolyte Attributes

Drought stress increased the proline contents (62.69%) and decreased the soluble sugars (30.60%), as compared to the control. Maximum soluble sugars (15.37 and 11.44 mg g-1 FW) at 0, 75, under control conditions (non-drought) and drought conditions, respectively, were observed when the foliar application of selenium at a rate of 6 mg/L was performed on lettuce plants (Figure 6).

3.7. Correlation Matrix

All the studied attributes were subjected to correlation analysis. The activities of enzymatic antioxidants, proline contents and electrolyte leakage were found to be negatively correlated with chlorophyll content, leaf dry weight, root dry weight and RWC. Positive correlations of enzymatic activities were noted with electrolyte leakage and proline content. Chlorophyll concentration was observed to be positively correlated with the measured parameters such as leaf dry weight, root dry weight, root length, shoot length and RWC (Table 1).

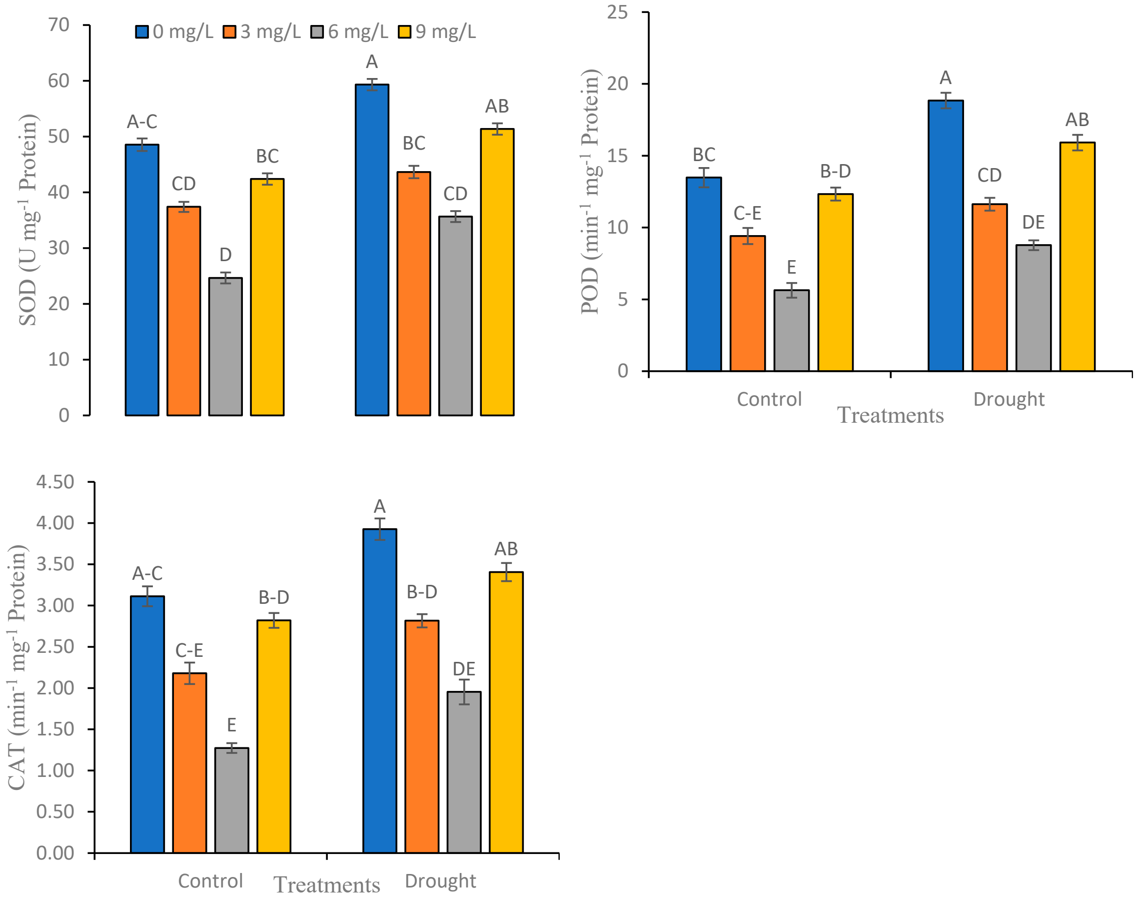

Figure 5. Enzymatic activities of lettuce treated with varying concentrations of foliar selenium (0, 3, 6 and 9 mg L^{-1}) under normal (85% ± 5%) and limited water regime circumstances (35% ± 5%). The uppercase letters in the bars denote significant differences between treatment means at $p \leq 0.05$ (Tukey's HSD); the values represent the means with standard deviation (SD) and were replicated three times.

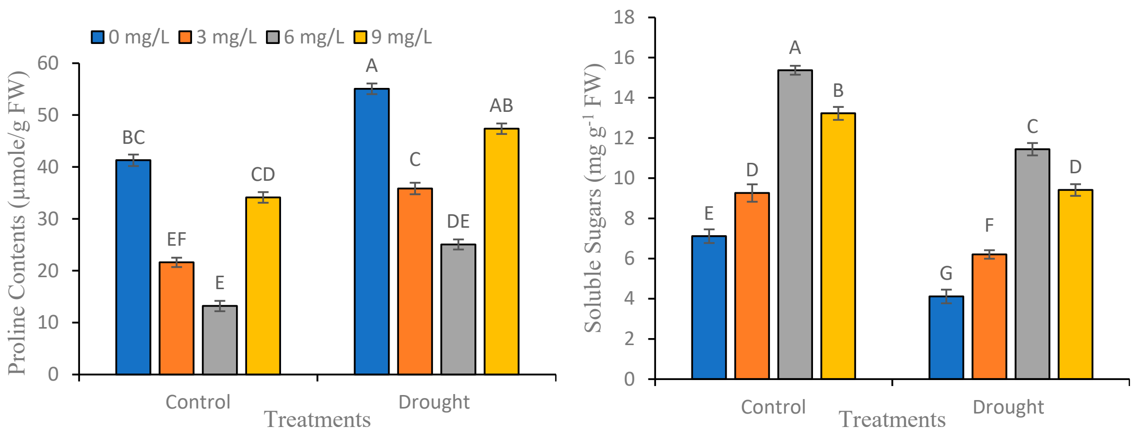

Figure 6. Osmolyte parameters of lettuce treated with varying concentrations of foliar selenium (0, 3, 6, and 9 mg L^{-1}) under normal (85% ± 5%) and limited water regime circumstances (35% ± 5%). The uppercase letters in the bars denote significant differences between treatment means at $p \leq 0.05$ (Tukey's HSD); the values represent the means with standard deviation (SD) and were replicated three times.

Table 1. Pearson correlation matrix of studied attributes of lettuce in response to various concentrations of foliar-applied selenium (0, 3, 6 and 9 mg L^{-1}) under normal and limited water regimes conditions.

Variables	*A*	CAT	CAR	*E*	EL	HW	LA	PFW	POD	PRO	RDW	RL	RWC	SDW	SL	SOD	SS	T CHL
CAT	−0.75 **																	
CAR	0.93 **	−0.68 **																
E	0.96 **	−0.78 **	0.92 **															
EL	−0.74 **	0.85 **	−0.67 **	−0.79 **														
HW	0.94 **	−0.73 **	0.94 **	0.93 **	−0.73 **													
LA	0.95 **	−0.72 **	0.87 **	0.91 **	−0.72 **	0.90 **												
PFW	0.95 **	−0.75 **	0.94 **	0.95 **	−0.73 **	0.98 **	0.91 **											
POD	−0.74 **	0.88 **	−0.69 **	−0.79 **	0.91 **	−0.75 **	−0.69 **	−0.74 **										
PRO	−0.76 **	0.91 **	−0.71 **	−0.80 **	0.93 **	−0.77 **	−0.75 **	−0.75 **	0.94 **									
RDW	0.96 **	−0.74 **	0.93 **	0.94 **	−0.72 **	0.97 **	0.91 **	0.98 **	−0.72 **	−0.75 **								
RL	0.93 **	−0.69 **	0.92 **	0.95 **	−0.65 **	0.90 **	0.87 **	0.91 **	−0.72 **	−0.75 **	0.67 **							
RWC	0.93 **	−0.68 **	0.93 **	0.92 **	−0.67 **	0.98 **	0.88 **	0.91 **	−0.67 **	−0.68 **	0.92 **	0.68 **						
SDW	0.97 **	−0.75 **	0.93 **	0.96 **	−0.72 **	0.92 **	0.90 **	0.94 **	−0.72 **	−0.74 **	0.95 **	0.94 **	0.93 **					
SL	0.93 **	−0.74 **	0.94 **	0.93 **	−0.70 **	0.96 **	0.90 **	0.95 **	−0.73 **	−0.75 **	0.94 **	0.94 **	0.94 **	0.92 **				
SOD	−0.76 **	0.94 **	−0.67 **	−0.80 **	0.90 **	−0.71 **	−0.73 **	−0.71 **	0.90 **	0.93 **	−0.71 **	−0.68 **	−0.64 **	−0.75 **	−0.72 **			
SS	0.97 **	−0.73 **	0.91 **	0.96 **	−0.72 **	0.90 **	0.91 **	0.93 **	−0.70 **	−0.73 **	0.94 **	0.92 **	0.91 **	0.98 **	0.89 **	−0.74 **		
T CHL	0.92 **	−0.69 **	0.87 **	0.93 **	−0.71 **	0.92 **	0.88 **	0.93 **	−0.73 **	−0.75 **	0.91 **	0.90 **	0.92 **	0.91 **	0.92 **	0.71 **	0.90 **	
gs	0.90 **	−0.60 **	0.88 **	0.88 **	−0.59 **	0.89 **	0.88 **	0.91 **	−0.61 **	−0.62 **	0.90 **	0.85 **	0.92 **	0.87 **	0.88 **	−0.59 **	0.88 **	0.88 **

** $p \leq 0.01$. RL—root length; SL—shoot length; LA—leaf area; PFW—plant fresh weight; HW—head weight; A—photosynthetic rate; E—transpiration rate; gs—stomatal conductance; CAT—catalase activity; T CHL—total chlorophyll content; EL—electrolyte leakage; RDW—root dry weight; PRO—proline content; SDW—shoot dry weight; CROs—carotenoid contents; RWC—relative water content; SOD—superoxide dismutase activity; SSs—soluble sugars.

3.8. Regression Analysis

Growth, biomass, physio-biochemical and water-related parameters were also tested using regression analysis (Figure 7). The R2 values of regressions were RWC and root dry weight, 95.43%; electrolyte leakage and total chlorophyll contents, 51.63%; plant fresh weight and SOD, 51.70%; root dry weight and gs association, 82.46%; soluble sugars and proline contents, 53.85%; and carotenoid contents and proline contents, 50.59%.

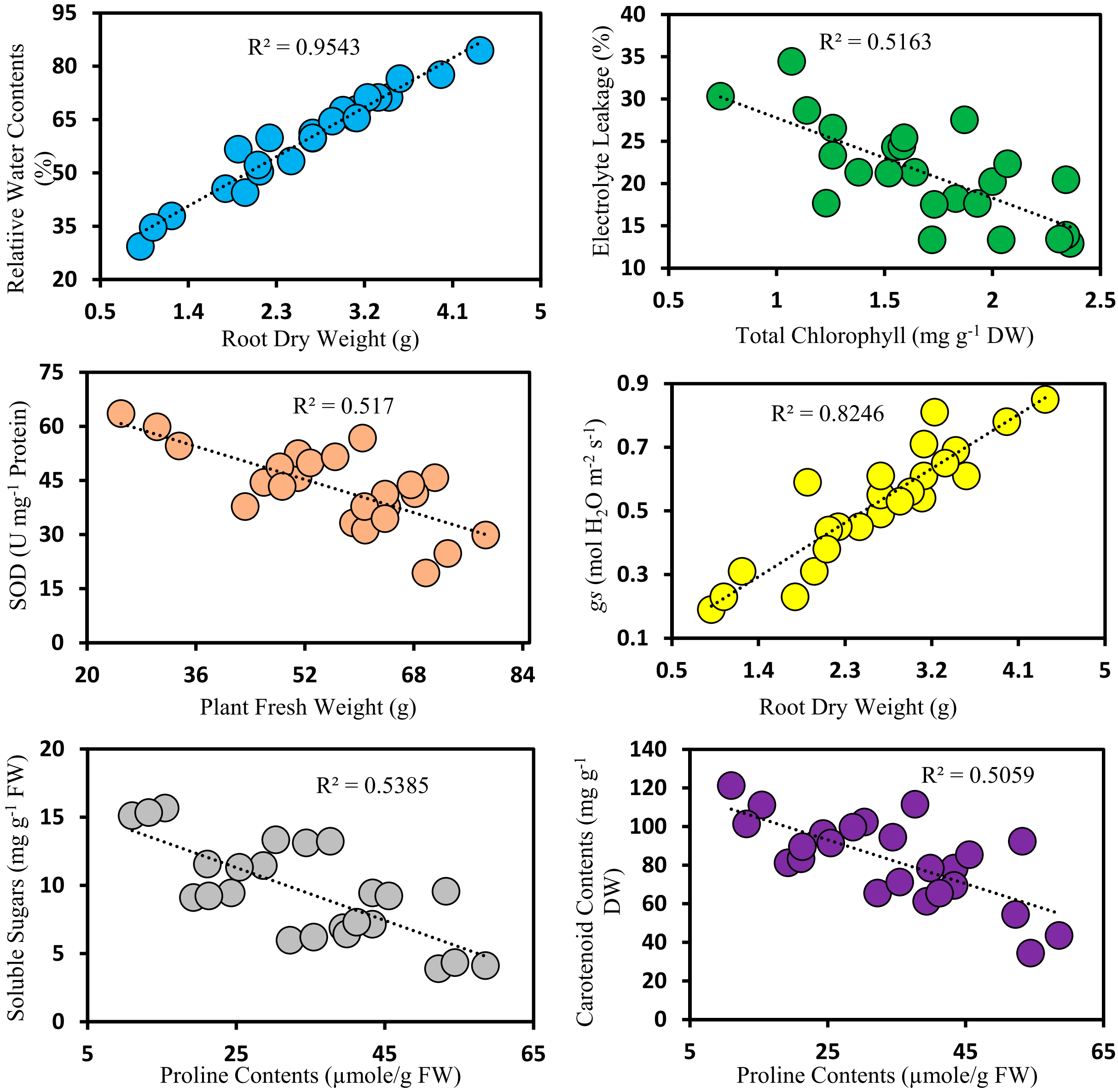

Figure 7. Scatter plots of various measured parameters with regression coefficient values.

3.9. Principal Component Analysis

Principal component analysis (PCA) was carried out to identify the grouping pattern among the measured variables based on agronomic and yield-related characteristics. The major cluster of parameters related to better growth and photosynthetic attributes plots in the positive PC1 quadrant. This group indicates a normal-to-healthy environment for plant development in terms of drought conditions and selenium levels. This includes attributes such as RFW, carotenoids, gs, chlorophyll b, soluble sugar and others. The second cluster plots in the negative sides of the PC1 and PC2 axis consist of SOD, CAT, EL, POD and proline. This cluster is classified as the enzymatic and osmolyte attributes of the lettuce plant, which are associated with stress-related responses. These attributes point to the generation of biomolecules when a plant is subjected to higher stress levels. The arrows show the increasing concentrations of selenium (Se) from the first group of plant enzymatic attributes towards the grouping of better growth and photosynthetic attributes (Figure 8).

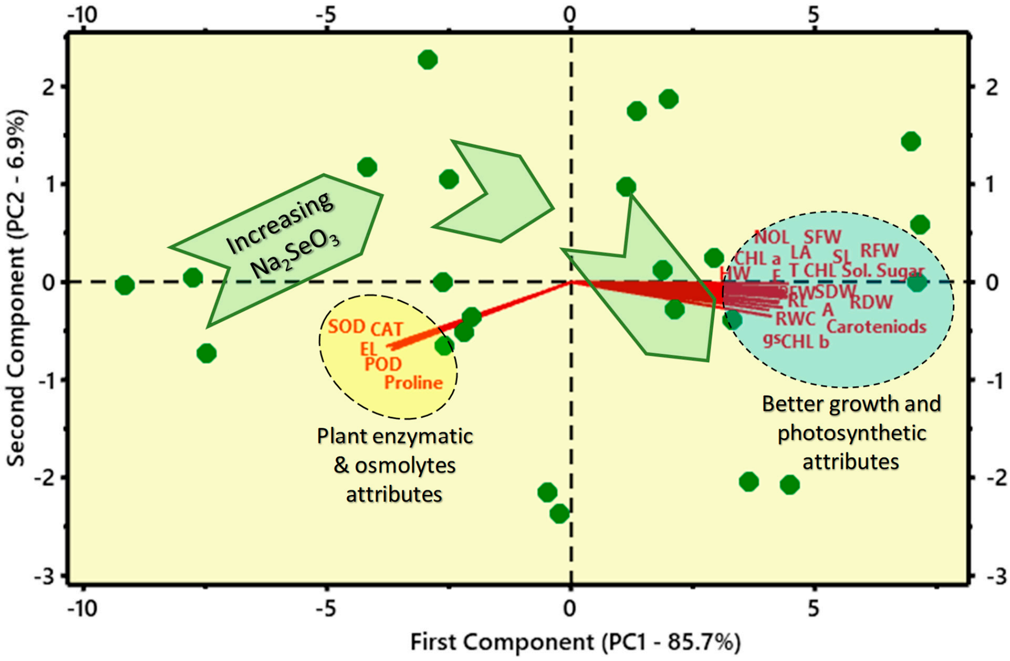

Figure 8. A graphical presentation of principal component analysis showing loadings (lines) and scores (circles) plots of various agronomic attributes of lettuce plants under drought and selenium stress conditions. Variability in measured attributes accounted for 92.6% variability.

4. Discussion

Under changing climatic scenarios, environmental extremes such as water scarcity (drought), salt stress and extreme temperature cause significant variations in physiological, molecular, morphological and biochemical processes in plants [35]. The growth, fresh and dry biomass of lettuce plants were significantly affected due to drought stress in our study. It was observed that when drought stress is applied, the cell size is decreased, and it also reduced the growth of plants [36]. Due to limited water flow from the xylem to the adjacent cells, which lowered cell elongation, water-limiting conditions lead to impaired cell elongation [37]. The availability of assimilates and the turgor pressure often determine how much the leaf expands [38]. Poor growth is caused by drought because it hinders cell elongation and mitosis [39,40]. According to Zhang et al. [41], the other major symptoms of drought stress include a lower number of leaves, branches twigs, and stems, the inhibition of root and shoot growth and decreased biomass. The application of mineral solutes at an appropriate level causes an improvement in the morphological and growth attributes of the lettuce plants by improving the negative impacts of drought stress [42,43]. In the current study, it was noted that after the exogenous application of Se in stressed plants, enhanced leaf area, improved growth and maximum fresh and dry biomass were noticed. It was observed that to enhance the cellular division of plant cells and for the elongation of cells, Se acts as a regulator compound [44] and can be considered a protective approach in order to cope with drought stress [45]. These results correlate with the findings of Karimi et al. [46], who documented that application of Se boosted the area of leaf in seedlings of wheat in stressed plants and non-stressed plants. These results may point to the simulative effect of Se application in enhancing root length and activity, leading to an increase in the plant's ability to absorb and move water and nutrients from the soil [47].

Photosynthetic attributes have high sensitivity to any biotic and abiotic stresses [48]. Studies have revealed that drought stress decreased porphobilinogen deaminase activity, which decreased the chlorophyll contents [49]. In the current study, electrolyte leakage (EL), which is a true indicator of stress sensitivity, was greater in drought-treated lettuce plants, as compared to the control. The overproduction and accumulation of ROS may be responsible for the improved lipid peroxidation, protein deprivation and severely hampered growth because of damaged DNA [50]. The present findings reveal that drought stress conditions significantly affected the photosynthetic attributes of lettuce plants compared with the control. The decreased photosynthetic rate in drought-stressed conditions is influenced due to the decreased stomatal conductivity and transpiration rate [51]. High stomatal conductivity and transpiration rates in tomatoes due to drought stress increase leaf cooling, giving improved defense for chlorophyll and retaining a relatively improved photosynthetic rate [52,53]. Due to drought stress, the reduction in the solubility of CO_2 to O_2 takes place in the tissues of leaves because of the lesser availability of CO_2 for the substrate [54]. In this study, Se enhanced the chlorophyll and carotenoid contents under drought-stressed and control conditions. Similar observations were also noticed in barley cultivars under drought stress regimes, possibly by protecting the chlorophyll pigments from oxidative damage through strengthening the level of carotenoids [55]. Foliar-applied Se enhances the defense system of a plant in order to cope with the damage caused by stress-induced ROS in the process of drought stress, which will, sequentially, assist in enhancing chlorophyll and carotenoid contents by limiting electrolyte leakage [46]. The enhanced photosynthetic activity and chlorophyll content in lettuce might be due to the better resistance to drought stress [56]. The outcomes of the present study are in line with the findings of Lanza et al. [57] and Skrypnik et al. [58], who found that leaf maturation, throughout which chloroplasts combined with chlorophylls break down, could be delayed with the application of Se, due to which photosynthesis, transpiration rate and enhanced photosynthetic efficiency can be achieved [59]. The increased size of chloroplasts and the maximum number of grana in the leaves might be due to foliar-applied Se, which enhances photosynthetic capacities in crop plants [60]. The optimal exogenous supplementation of selenium increased chlorophyll pigment and its biosynthesizing enzyme activity in plant tissues even in cases of extreme drought stress by reducing ROS production, which is partially responsible for the quenching of photosynthetic pigments [61].

The formation of numerous non-enzymatic and enzymatic ROS-scavenging and detoxification systems increases the ability of tolerant plants against the injurious effects of ROS [62]. Mukarram et al. [63] observed that the enzymatic antioxidant displayed a preliminary increase under drought stress. The activities were also condition-dependent due to their tolerance or susceptibility to several crop types, stages in the growth process and the growing season [64]. An antioxidant system in plants is formed by the usage of the enzymes POD, CAT and SOD to eradicate the excess of ROS induced by stress, thus defending the cells from the lethal effects of oxidation reactions [65]. CAT, SOD and the antioxidants POD are recognized for the dismutation of hydrogen peroxide to water and molecular oxygen in cells [30]. It was observed that the activities of the eliminating enzymes of ROS changed meaningfully in lettuce plants under drought-stressed and control conditions. However, during normal growth conditions, without Se, plants showed greater enzymatic antioxidant activity when compared to foliar-applied Selenium plants. This inexperienced parameter of CAT activity has been testified in numerous revisions [66].

Drought stress led to preventing the integration of CO_2 and reducing the integrated supply in lettuce plants, consequently decreasing soluble sugars and increasing the proline contents in the lettuce plants [67]. Moreover, foliar-applied Se plants showed an improvement in enzymatic activities during drought stress compared to normal conditions. This enhancement may be related to selenium's essential function in promoting the gene expression in charge of the antioxidant defense system, which, in turn, raised the SOD, CAT and POD activities and improved the tolerance of drought stress in plants [57]. Furthermore, Se led to an improved sugar yield and decreased proline contents, especially in improving lettuce as a storage sink for nutrient elements, for example, carbon and nitrogen, and as a scavenger for free radicals, resulting in decreased proline [68]. The activation of the enzymes that aid in the detoxification of O^{-2}, H_2O_2 and lipid peroxidation, in terms of membrane leakage, and reduce the generation of a very toxic OH may also be attributed to the substantially antagonistic influences of the Se element due to ROS overproduction [69]. Increased RWC concentration has been discovered to be directly connected to increased soluble sugar content, which also boosts plant tolerance to drought-stressed circumstances [54]. The optimal level (dose) and suitable Se salt is beneficial for improving abiotic stress tolerance in crop plants. However, higher levels cause toxicity and limit plant growth and development [57].

5. Conclusions

Drought stress reduced the growth, phenological and biomass-related traits and enhanced electrolyte leakage in lettuce plants. The exogenous application of Se in an appropriate amount promoted growth and biochemical attributes by decreasing electrolyte leakage and improving the enzymatic antioxidant defense system of lettuce plants. Plants exposed to Se under drought conditions had enhanced RWC, enzymatic activity, soluble sugars, photosynthetic pigment levels and fresh and dry biomass, as compared to control plants. In response to drought stress, lettuce plants produce more antioxidants, which counteracts the negative effects of drought stress on biomass accumulation. Based on the findings of this study, it can be concluded that foliar Se supplementation is more effective at minimizing the adverse effects of irrigation water shortage situations. We recommend conducting field studies on water quality and confirming the negative effects of selenium on lettuce growth and yield under multiple abiotic stresses. Prior to making a commercial recommendation, economic factors must be taken into account.

Author Contributions: Conceptualization, Q.u.Z., A.A. and B.T.; methodology, B.T. and K.A.; software, K.S.; validation, A.A., K.S. and Q.u.Z.; formal analysis, B.T.; investigation, Q.u.Z.; resources, B.T.; data curation, B.T. and T.M.; writing—original draft preparation, A.A., H.M.A. and K.A.; writing—review and editing, M.T.K., T.M. and Q.u.Z.; visualization, K.S. and M.T.K.; supervision, Q.u.Z.; project administration, H.M.A. and Q.u.Z.; funding acquisition, H.M.A. and A.A. All authors have read and agreed to the published version of the manuscript.

Funding: This work was funded by the Researchers Supporting Project number (RSP2023R123), King Saud University, Riyadh, Saudi Arabia.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Not applicable.

Acknowledgments: The authors would like to extend their sincere appreciation to the Researchers Supporting Project number (RSP2023R123), King Saud University, Riyadh, Saudi Arabia.

Conflicts of Interest: The authors declare no conflict of interest.

Abbreviations

Se	Selenium
POD	Peroxidase Activity
SOD	Superoxide Dismutase activity
CAT	Catalase Activity
FW	Fresh Weight
DW	Dry Weight
TW	Turgid Weight
EC	Electrical Conductivity
RWC	Relative Water Contents
HSD	Highest Significant Difference

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