



Article

Morphological and Biochemical Response of *Potatoes* to Exogenous Application of ZnO and SiO₂ Nanoparticles in a Water Deficit Environment

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Abstract: A field study was conducted to understand the effectiveness of foliar applications of ZnO-NPs (0, 50, 100 mg L⁻¹) and SiO₂-NPs (0, 25, 50 mg L⁻¹) on potato plant growth, morphology, nutrient uptake, oxidative stress, and antioxidative response under drought conditions (i.e., 100% crop evapotranspiration ET_c, 75% ET_c, and 50% ET_c). Results revealed that water deficiency significantly hampered plant growth and biomass production and stimulated oxidative stress in potatoes. However, the exogenous application of ZnO-NPs and SiO₂-NPs significantly improved plant growth attributes such as the number of branches, plant height, fresh and dry biomass, leaf area, and leaf area index as compared with untreated plants. The foliar application of ZnO-NPs (i.e., 100 and 50 mg L⁻¹) and SiO₂-NPs (50 mg L⁻¹) promoted the mineral ion accumulation in plants grown under water deficiency and thus resulted in higher NPK, Zn²⁺, Fe²⁺, and Mn²⁺ contents. A significant reduction in malondialdehyde (MDA) and hydrogen peroxide (H₂O₂) was found in plants treated with 100 mg L⁻¹ ZnO followed by 50 mg L⁻¹ SiO₂ and 50 mg L⁻¹ ZnO nanoparticles as compared with untreated plants, respectively. Furthermore, the aforesaid treatments resulted in the maximum activity of antioxidant enzymes (i.e., superoxide dismutase SOD, catalase CAT, polyphenol oxidase PPO, and ascorbate peroxidase APX) under water deficit stress. Similarly, the foliar application of ZnO and SiO₂ nanoparticles improved nonenzymatic antioxidants such as total flavonoid content (TFC) and total phenolic compounds (TPC) as compared with untreated plants (control). Moreover, plant growth traits were significantly and positively correlated with mineral contents, while they were negatively correlated with MDA and H₂O₂. ZnO-NPs and SiO₂-NPs applications improved biochemical traits, which might lead to enhancements in plant tolerance and improvements in potato growth, productivity, and quality traits under water shortage conditions.

Keywords: *Solanum tuberosum*; antioxidants; ZnO-NPs; SiO₂-NPs; oxidative stress; plant growth; water shortage



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1. Introduction

The world's population has increased in the last few decades, and food demand has increased accordingly, which heavily requires more irrigated land to maintain an adequate food supply [1]. Water deficiency/shortage is one of the major abiotic factors that adversely affects plant growth and production globally [2,3]. In addition, climatic change may increase the evapotranspiration rate [4]. Therefore, half of the arable lands are expected to have serious problems by 2050 due to water stress [5]. Water shortage greatly affects a wide range of complex morphological and biochemical events in higher plants [6,7]. Plant vegetative traits such as leaf area and plant height are reduced under water shortage conditions [8,9]. A water-deficient environment negatively affects the mineral uptake

by roots, osmoregulation, chemiosmotic balance, and translocation of mineral ions to arial parts [10–12]. Thus, stimulated oxidative stress in plants, overproduction of reactive oxygen species (ROS), and lipid peroxidation of cellular membranes escalate the associated implications of water deficit stress in plants [10,11].

Plants exposed to abiotic stresses typically have an antioxidant defense system that protects them by scavenging ROS. This homeostatic mechanism works by using non-enzymatic flavonoids and phenolic compounds [13,14] and antioxidant enzymes such as superoxide dismutase (SOD), peroxides (POD), polyphenol oxidase (PPO), and catalase (CAT) [15–17]. Antioxidants are both enzymatic and non-enzymatic molecules that help stabilize cells by removing excess ROS [12]. Under water shortage conditions, an increase in flavonoid and polyphenolic contents was observed in cucumber (*Cucumis sativus* L.) [18].

Currently, nanoparticles (NPs) are being used as nanofertilizers due to their novel properties, such as their small size, high efficiency, and low phytotoxicity levels [19]. Exogenous application of NPs has recently gained scientific attention due to their ability to (a) mitigate the abiotic stress effects; (b) increase the contents of antioxidant enzymes; (c) improve physiological processes; and (d) improve nutrient uptake under environmental stresses in agricultural crops [20,21]. Nanoparticles are capable of increasing antioxidants, thereby reducing H₂O₂ and malondialdehyde production [22]. Their uniqueness in nature, shapes, and dimensions enable them to enter plants through both leaves and roots, translocate via either the symplastic or apoplastic pathways, and thus stimulate enzymatic activity at cellular levels [23].

Zn is a component of some biomolecules as well as a cofactor for auxins and metabolic enzymes. It enhances plant vegetative growth traits and increases tolerance to both biotic and abiotic stresses [24]. Plants treated with ZnO-NPs showed lower levels of ROS and lipid peroxidation, which reflects a significant correlation between enhanced antioxidant activity and reduced oxidative stress [25]. Recent literature has highlighted the role of ZnO-NPs as abiotic stress mitigators and growth regulators, especially under drought and saline stress [26,27]. Application of ZnO-NPs improves drought tolerance in tomatoes and eggplant [27–30].

Silicon (Si) is the second-most abundant element on earth. Even though it is not classified as an essential element for plants, The International Plant Nutrition Institute has recently implicated it as a “quasi-essential” element [31]. Moreover, Si improves crop performance under biotic and abiotic stresses [32]. Silica nanoparticles (SiO₂-NPs) can play a pivotal role in alleviating abiotic stresses such as salinity and drought [33]. The growth, nutrient uptake, and productivity traits of cucumber (*Cucumis sativus* L.) plants treated with SiO₂-NPs under water stress conditions were significantly improved in comparison with non-treated plants [34].

Potato is the largest vegetable crop extensively grown in 150 countries of the world ranging from 65° N to 50° S latitude [35]. The total cultivated area of potatoes in 2021 was estimated to be 18.133 M ha. Potatoes are a vital source of nutrients, vitamins, minerals, amino acids, carbohydrates, proteins, and antioxidants essential for ATP production and the nutrition of the human body [36]. However, water shortages are significantly impacting potato growth and productivity [37]. Furthermore, potato plants have shallow root systems, making them extremely sensitive to water stress [38].

Therefore, the objective of this study was to investigate the influence of exogenous/ foliar application of ZnO-NPs and SiO₂-NPs on potato plants under water shortage conditions on morphological traits and mineral contents. In addition, biochemical traits, including oxidative damage and the antioxidant system, were evaluated. It was hypothesized that the foliar application of ZnO and SiO₂ nanoparticles may improve potato growth by facilitating stress tolerance and antioxidant mechanisms under water-deficit conditions.

2. Materials and Methods

2.1. Nanoparticles [ZnO and SiO₂] Characterization

Nanoparticles of ZnO and SiO₂ were purchased from Sigma-Aldrich (St. Louis, MO, USA). The morpho-structural properties of both ZnO and SiO₂ nanoparticles were determined using scanning electron microscope (SEM) coupled with energy dispersion X-ray spectroscopy (EDX) and transmission electron microscope (TEM). ZnO-NPs were found to have a quasi-spherical to hexagonal wurtzite shape, but a few non-spherical monoclinic particles were also found, whereas the SiO₂-NPs were nearly spherical in shape with non-smooth surfaces (Figure 1A,B). The results obtained from elemental dispersive spectroscopy (EDS) showed strong signals for zinc (Zn) and oxygen (O), which confirmed that ZnO-NPs are fundamentally made up of Zn and O elements (Figure 1C). Likewise, strong signal peaks were observed for Si and O in case of SiO₂ analysis, which evidently supported the elemental nature of SiO₂-NPs (Figure 1D). Crystalline structure of ZnO- NPs and SiO₂- NPs were determined using X-ray diffraction (XRD) with Cu K α radiation ($\lambda = 1.5406 \text{ \AA}$) operated at voltage of 40 kV and current of 15 mA [39]. Furthermore, Figure 2A shows the fourier transmission infrared (FTIR) of ZnO NPs, where a sharp peak was observed at 494 cm^{-1} , attributed to zinc-oxygen (Zn-O) stretching vibration mode. Additionally, the broad absorption bands observed at 3425 cm^{-1} and 1630 cm^{-1} were due to the presence of -OH groups of water that were adsorbed on the ZnO NPs surface. In Figure 2B, the FTIR of SiO₂ NPs showed an observed sharp peak at 1099.32 cm^{-1} which was attributed to the asymmetric stretching and bending vibrations of Si-O-Si. The broad absorption bands observed at 3453 cm^{-1} and 1630 cm^{-1} were due to the presence of -OH groups in SiO₂ (adsorbed water molecules). The peak at 804 cm^{-1} indicates in-plane bending vibrations of geminal groups.

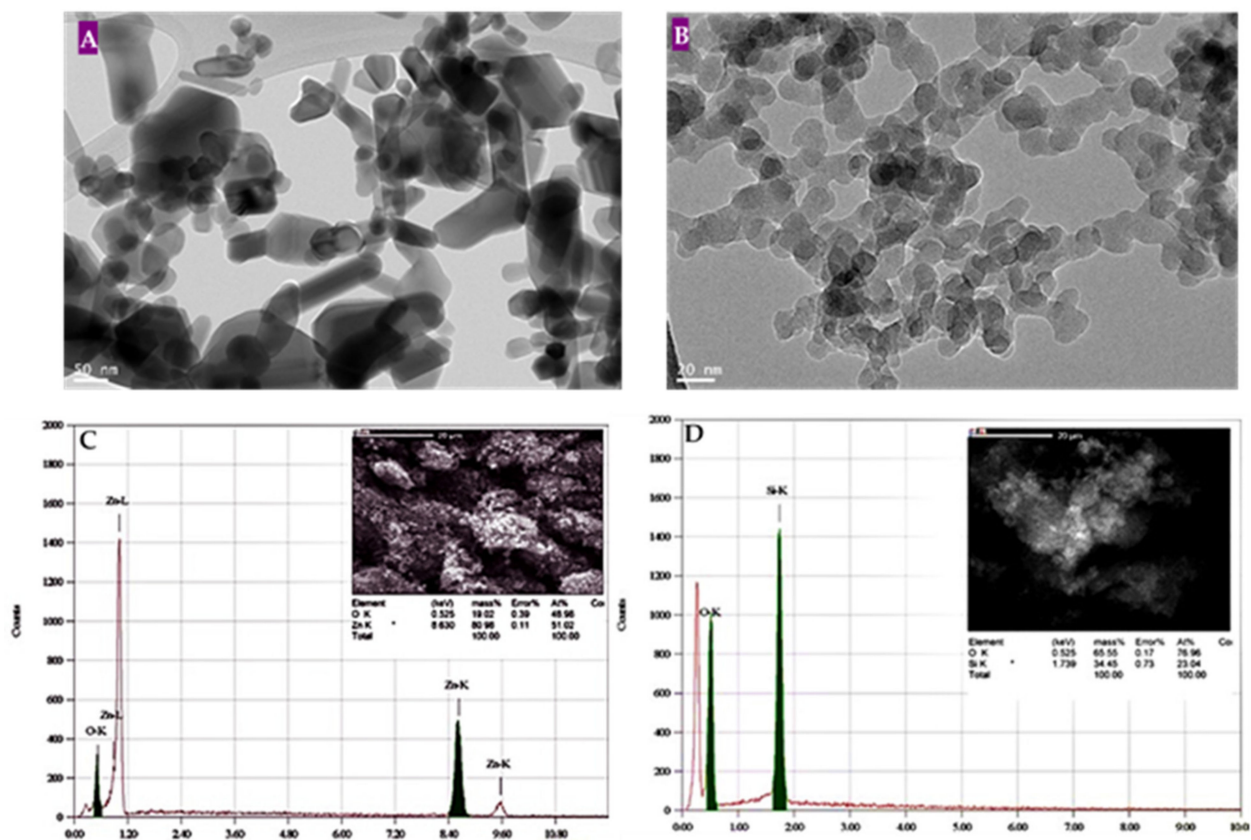


Figure 1. TEM of ZnO-NPs (A) and SiO₂-NPs (B). EDS (Elemental dispersive spectroscopy) spectrum of ZnO-NPs (C) and SiO₂-NPs (D).

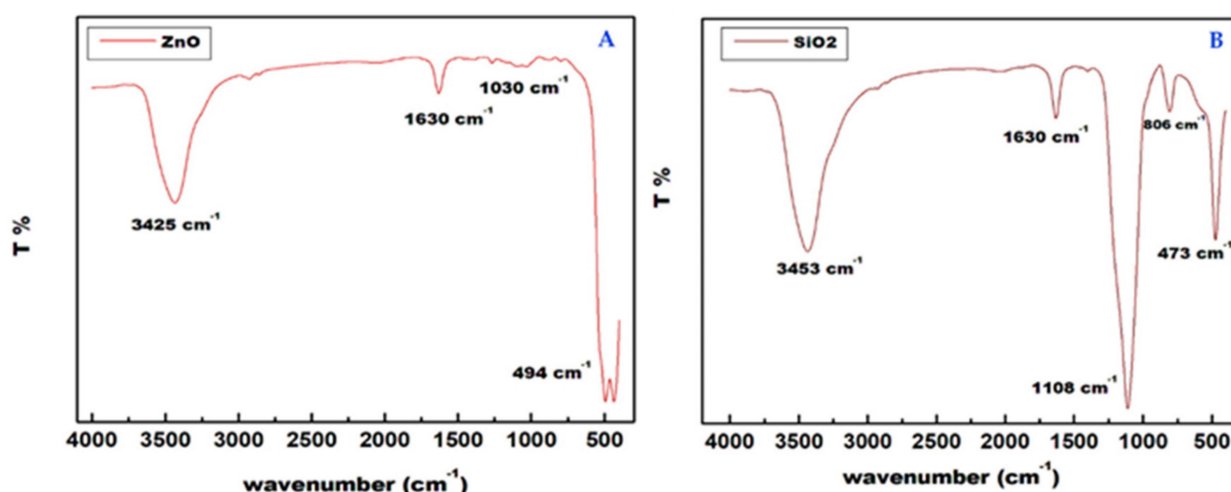


Figure 2. FTIR (Fourier transform infrared spectrum) of ZnO-NPs (A), and SiO₂-NPs (B).

2.2. Experimental Materials, Setup and Design

The current experiment was performed at Agriculture Research Farm, College of Food and Agriculture Sciences, King Saud University, Riyadh, Saudi Arabia (46°36′51″ E, 24°43′36″ N, 665 masl). Air temperature and relative humidity (Figure 3) were recorded from an onsite automatic weather station. The mean air temperature was 25.27 °C and the mean relative humidity was 32.60% during the experimental period. Reference evapotranspiration (ET₀) was calculated according to Penman–Monteith [40], using the daily environmental data of the experimental site. Furthermore, soil physico-chemical traits were analyzed to a depth of 45 cm (Table 1).

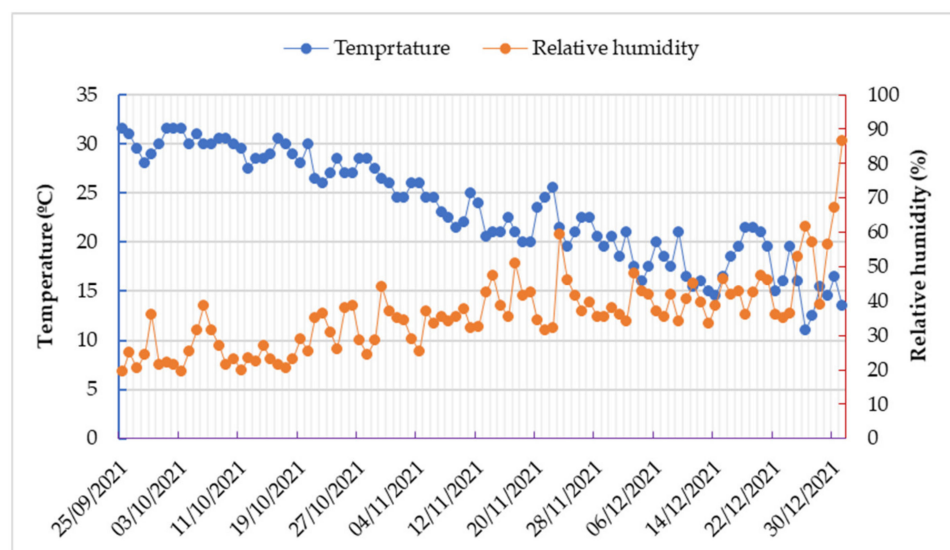


Figure 3. Mean air temperature and relative humidity throughout the growing season.

Table 1. Physicochemical properties of experimental soil.

Particle Size Distribution (%)			Texture Class	FC (%)	WP (%)	OM (%)	Ks (mm/h)	ρ_b (g cm ^{−3})	pH	EC (dS/m)
Sand%	Silt%	Clay%								
83.72	7.83	8.45	Sandy Loam	14.9	6.7	0.83	24.8	1.6	7.8	1.98

FC: field capacity; WP: wilting point; O.M: Organic matter; Ks: saturated conductivity; and ρ_b : bulk density.

Certified seeds of potato (*Solanum tuberosum* L. cv. Hermes) were obtained from the Saudi Agricultural Development Company, Riyadh, Kingdom of Saudi Arabia. The potato tubers, with an average weight of 59–64 g, were planted on 25 September 2021. Potato tubers were planted at 40 cm plant-to-plant distance in 100 cm-apart rows, where all cultural practices were performed as recommended [41]. The experiment was designed as a split-plot arrangement in randomized complete block design (RCBD), and all treatment units were replicated three times. Different drip irrigation levels [(100% crop evapotranspiration (ET_c), 75% ET_c, and 50% ET_c)] were assigned to main plot 35 days after planting, and the sub-plots were provided with different exogenous applications of nanoparticles (ZnO-1 = 50 mg L⁻¹, ZnO-2 = 100 mg L⁻¹, and SiO₂-1 = 25 mg L⁻¹, SiO₂-2 = 50 mg L⁻¹, and control). Where the crop water requirement as crop evapotranspiration (ET_s) was computed using the reference evapotranspiration rate (ET_o) and crop coefficient (K_c). Foliar applications of ZnO and SiO₂ nanoparticles were carried out twice, at 45 and 65 days after planting.

2.3. Data Recorded

2.3.1. Morphological and Growth Traits

Five plants from each subplot were randomly taken for measurements of morphological traits. Plant height and number of lateral branches were counted for the selected plants. Leaf area per plant was measured using LI-COR portable area meter (Model LI-3000A, LI-COR, Lincoln, NE, USA). The leaf area index (LAI) was computed using the formula described by Watson [42].

$$LAI = \frac{\text{Total leaf area of the plant}}{\text{Ground area Occupied by plant}} \quad (1)$$

Shoot fresh weight was weighted in grams per plant. Fresh shoot samples of 100 g were dried in forced air oven at +70 °C until the dry weight became constant.

2.3.2. Mineral Concentrations in Potato Leaves

Leaves from potato plants were taken randomly from each treatment. The samples were oven dried for 48 h at 75 °C and then pulverized as smooth powder for the determination of the following minerals:

Nitrogen

Leaf nitrogen contents (N) were determined using Kjeldahl digestion method as described by Munoz-Huerta et al. [43].

P, K¹⁺, Zn²⁺, Mn²⁺, and Fe²⁺

Sulfuric acid (5 mL) and hydrogen peroxide (H₂O₂) were used to digest 0.2 g dried leaf samples. The mixture was heated at 200 °C for 15 min using thermal plate, and 0.5 mL of H₂O₂ was added while continuing to heat the mixture until clear solution was obtained [44]. The solutions were then filtered, and extracts were preserved in airtight plastic bottles for further use. Optical spectrophotometry technique [45] was used to determine phosphorus contents, whereas inductively coupled plasma optical emission spectrometry (ICP-OES) was used for cations such as K¹⁺, Zn²⁺, Mn²⁺, and Fe²⁺ [46].

2.4. Enzymatic Component

2.4.1. Enzyme Extraction

For the assessment of different enzymatic activities, randomly selected leaf samples were collected and stored at −80 °C. To extract the crude enzymes, 200 mg leaf samples were homogenized in liquid nitrogen to prevent proteolytic activity. The mixtures were then dissolved in 100 mM phosphate buffer made up of 0.1 mM Ethylenediaminetetraacetic acid (EDTA), 0.5% (v/v) Triton-X 100, and 0.1% (w/v) polyvinylpyrrolidone (PVP) at 7.0 pH.

The reaction mixture was centrifuged for 20 min ($10,000 \times g$) at $4\text{ }^{\circ}\text{C}$ [47,48]. Supernatant fraction was collected for the determination of various enzymatic activities and total soluble proteins, as described by Bradford [49].

2.4.2. Enzyme Assay

The enzymatic activity of superoxide dismutase (SOD) was determined using the method of Hammerschmidt et al. [50]. A reaction mixture made up of 1.5 mL of 0.1 M Na^+ phosphate buffer (pH 7.0), 1 mL of 0.25 mM pyrogallol, 0.5 mL EDTA, and 100 μL enzymatic extract was prepared, and the absorbance was observed at 420 nm for 120 s in spectrophotometer and expressed in unit/mg protein (U mg^{-1} protein). Where one unit (U) was taken as the amount of enzyme needed for 50% inhibition of pyrogallol oxidation. To determine the peroxidase (POD) activity, a reaction mixture of 220 μL of 100 mM phosphate buffer (pH 7.0) at $20\text{ }^{\circ}\text{C}$, 220 μL of 5% (*w/v*) pyrogallol solution, 100 μL of 0.50% (*w/w*) hydrogen peroxide solution (H_2O_2), 3 μL of enzyme solution, and 1.4 mL distilled water was prepared and incubated for 5 min at $25\text{ }^{\circ}\text{C}$, and the absorbance was then measured at 420 nm according to the method described by Kong et al. [51]. Catalase (CAT) activity (U mg^{-1} protein) was estimated from a reaction mixture of 0.1 M phosphate buffer (pH 7.0), 1.0 mL of 0.059 M H_2O_2 , 1.9 mL of distilled water, and 100 μL of enzyme solution observed at 240 nm [52]. Polyphenol oxidase (PPO) was determined using the method described by Malick and Singh [53]. The absorbance was measured spectrophotometrically at 40 nm, and enzymatic activity was calculated. Ascorbate peroxidase (APX) activity was estimated by the decrease in absorbance at 290 nm. A reaction mixture of 1.0 mL of the buffer contained 100 μL of 0.5 mM ascorbate, 100 μL of 3 mM H_2O_2 , 100 μL of 0.1 mM EDTA, and 100 μL enzyme extract. It was allowed to run for 2 min at $25\text{ }^{\circ}\text{C}$ [54]. The activity of APX was computed by using the extinction coefficient of $2.8\text{ mM}^{-1}\text{ cm}^{-1}$.

2.5. Non-Enzymatic Component

2.5.1. Total Flavonoid Content (TFC)

The total flavonoid contents were determined using the method described by Ordonez et al. [55]. A 0.5 mL of 2% AlCl_3 water solution was added to 0.5 mL of methanol extract of potato leaves. The mixture was left for 24 h at room temperature, and then the absorbance was determined at 420 nm by spectrophotometer UV–1800 (SHIMADZU, Tokyo, Japan). The calibration curve with quercetin standard (50–400 $\mu\text{g/mL}$) and linear relation as $y = 0.0173x + 0.0134$ was used to calculate TFC and expressed as quercetin ($\text{mg QE g}^{-1}\text{ DW}$).

2.5.2. Total Phenolic Content (TPC)

The total phenolic content was determined according to Ainsworth et al. [56] using Folin–Ciocalteu reagent. The TPC was calculated as mg gallic acid equivalent in dry-weight plant sample ($\text{mg GAE g}^{-1}\text{ DW}$).

2.6. Oxidative Stress Biomarkers

2.6.1. Lipid Peroxidation (Malondialdehyde ($\text{C}_3\text{H}_4\text{O}_2$))

Lipid peroxidation was determined by calculating the rate of malondialdehyde (MDA), as illustrated by Rao and Sresty [57]. Fresh samples (200 mg of leaf) were collected and ground with liquid nitrogen, then homogenized in 5 mL of 0.1% TCA (trichloroacetic acid; $\text{C}_2\text{HCl}_3\text{O}_2$), and the mixture was centrifuged for 10 min at $10,000 \times g$. The supernatant (1.0 mL) was mixed with 5 mL of 0.5% thiobarbituric acid (TBA) and 4 mL of 20% TCA and heated at $95\text{ }^{\circ}\text{C}$ for 30 min, followed by ice-shock. The samples were centrifuged for 10 min at $10,000 \times g$. Using a spectrophotometer UV–1800 (SHIMADZU, Japan), the supernatant absorbance was estimated at 450, 532, and 600 nm as OD450, OD532, and OD600, respectively. The malondialdehyde content was computed by the following formula:

$$\text{MDA}(\mu\text{mol g}^{-1}\text{FW}) = 6.45(\text{OD532} - \text{OD600}) - 0.56(\text{OD450}) \quad (2)$$

2.6.2. Hydrogen Peroxide (H₂O₂)

Fresh samples (200 mg leaf tissues) were homogenized with 2 mL of 0.1% (*w/v*) trichloroacetic acid (TCA), and crude extract was centrifuged for 15 min at 12,000× *g*. A mixture of 1.0 mL of 1.0 M of potassium iodide (KI), 0.5 mL of 10 mM potassium phosphate buffer (pH 7.0), and 0.5 mL of supernatant was prepared, and absorbance was measured at 390 nm to estimate hydrogen peroxide content as described by Velikova et al. [58].

2.7. Statistical Analysis

The data obtained from exogenous application of ZnO-NPs and SiO₂-NPs on potato plants under water shortage conditions were subjected to the analysis of variance (ANOVA) at $p \leq 0.05$, where treatment means were differentiated using Tukey's test by SAS (version 9.2, SAS Institute, Inc., Cary, NC, USA). The principal component analysis (PCA) and Pearson's correlation were performed using XLSTAT statistical package software (Version 2019.1, Excel Add-ins soft SARL, New York, NY, USA).

3. Results and Discussion

3.1. Morphological and Growth Traits

All tested morphological and growth traits, such as plant height, fresh and dry shoot weights, number of branches, leaf area, and leaf area index (LAI), of potato plants were significantly reduced under 75% ETc and 50% ETc water treatments as compared with the control (100% ETc) treatment (Figure 4). Canopy growth is among the most sensitive phases in plants under water deficit stress [59]. Water shortage has been recurrently reported to inhibit plant height, number of branches, shoot fresh weight and shoot dry weight [60–62], and leaf area [63] in potatoes. Drought significantly reduced the leaf area index of potato plants [64]. Nevertheless, ZnO-NPs and/or SiO₂-NPs increase plant height, number of branches, leaf area, and shoot fresh and dry weights in comparison with the control treatment. However, among all foliar applications, ZnO-NPs at 100 mg L^{−1} stood significantly better treatment, followed by ZnO-NPs at 50 mg L^{−1} and SiO₂-NPs at 50 mg L^{−1}, respectively (Figure 4). The increase in fresh and dry weights can be associated with the role of NPs in promoting photosynthetic activity by improving photolysis of water and oxygen evolution [65]. NPs may also increase PSI and PSII activity, possibly improving net CO₂ assimilation and subsequent biomass production [66]. These increases in photosystem activity are mostly due to the effect of NPs on promoting the overexpression of photosynthesis-related genes at the cellular level [67]. NPs, in general, form complexes with light-harvesting complex proteins (LHC) and enhance light harvesting [68]. NPs promote photosynthetic activity by increasing CO₂ assimilation, the fundamental process of biomass production essential for plant growth [65]. The exogenous applications of ZnO-NPs improved all growth and dry biomass traits in tomato [69,70], wheat [71], and peanut [72] plants. On the other hand, SiO₂-NPs increased plant growth traits in stressed plants [73,74]. According to Siddiqui and Al-Wahaibi [75], the application of nano-SiO₂ significantly improved the fresh and dry weight of tomato plants. Even though in the current study the exogenous application of both ZnO-NPs and SiO₂-NPs significantly improved all studied growth attributes as compared with control (CK), especially under 75 and 50% ETc treatments, the ZnO-NPs performed significantly more efficiently in mitigating the water deficit stress in potato plants.

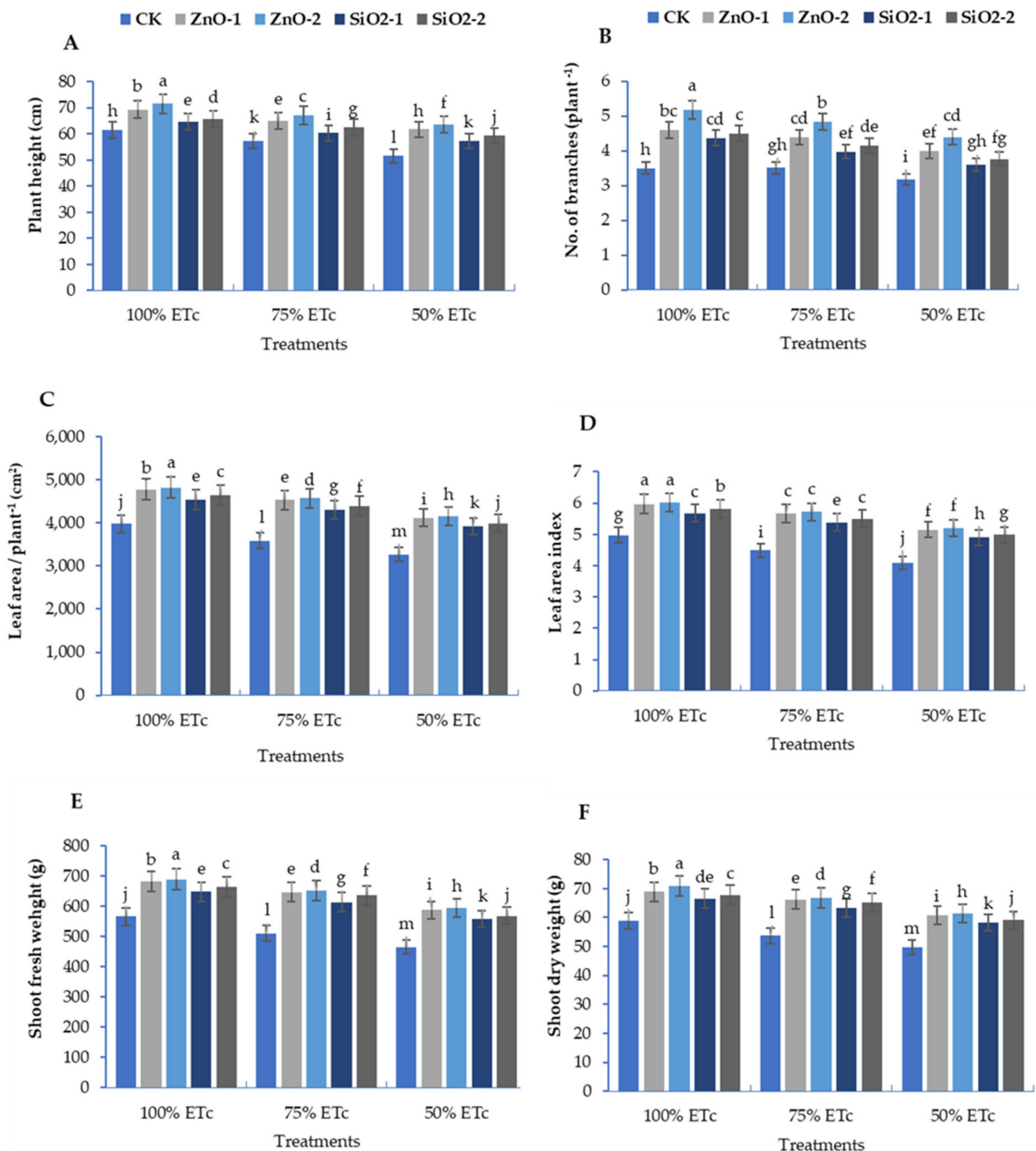


Figure 4. Effect of ZnO and SiO₂ NPs on plant height (A), number of branches (B), leaf area (C), leaf area index (D), shoot fresh weight (E), and shoot dry weight (F) of potato plants grown under different water deficit treatments. Nanoparticle doses: CK (control), ZnO-1 (50 mg L⁻¹), ZnO-2 (100 mg L⁻¹), SiO₂-1 (25 mg L⁻¹), and SiO₂-2 (50 mg L⁻¹). Bars with different letters indicate significant differences between mean values according to Tukey's test at $p \leq 0.05$.

3.2. Mineral Contents

Macronutrients and micronutrients in potato leaf tissues significantly decreased under water shortage (Figure 5). The lowest concentrations of these minerals as compared with unstressed plants (100% ETc) were recorded in 50% ETc. Water shortages make it difficult

for plants to absorb nutrients due to restricted mass flow and cause symptoms of nutrient deficiency [76]. Furthermore, water deficit stress reduces nutrient content, particularly NPK, in stressed plants as compared with controls [11]. Water shortages may have a negative impact on NPK content due to reduced nutrients' uptake and translocation through the xylem [77,78]. Similar findings were also reported by Dawa et al. [79] and Ragab et al. [80] for the tomato hybrid "Marwa" under water deficit conditions. The foliar application of ZnO and SiO₂ nanoparticles significantly increased the N, P, K¹⁺, Zn²⁺, Mn²⁺, and Fe²⁺ content in potato leaves as compared with control (CK) (Figure 5). Application of ZnO-NPs at 100 mg L⁻¹, ZnO-NPs at 50 mg L⁻¹, and SiO₂-NPs at 50 mg L⁻¹, respectively, led to the best results of NPK and Zn²⁺, Mn²⁺, and Fe²⁺ contents in stressed plants compared with other treatments. Nanomaterials improve water and nutrient absorption and the activity of antioxidant enzymes, which enhance plants' tolerance to stress conditions [81]. NPs promote the production of organic acids exuded by the root, primarily oxalic, citric, lactic, and fumaric acids, which promote nutrient absorption by plants by creating negative water potential (hypertonic) in root tissues. Such a homeostatic mechanism helps plants adjust plant water relations under drought stress [82]. The exogenous application of ZnO-NPs improved the uptake of N, P, K¹⁺, and Zn²⁺ in tomato leaves, where the highest values were recorded for 100 mg L⁻¹ ZnO treatment [6]. It was reported that water stress reduced eggplant nutritional contents; however, the foliar spray of ZnO-NPs alleviated these negative impacts significantly [27]. On the other hand, silicon fertilization enhances nutrient uptake during water-deficient conditions [83]. A number of studies have reported that Si application in plants under water deficit stress can play an important role in mineral ions' uptake, transportation, and distribution within the plant [84]. Likewise, foliar application of Si-NPs increased K, Fe, Zn, and Mn concentrations in tomato leaves [85,86]. Comprehensively, the foliar application of ZnO-NPs in comparison with SiO₂-NPs, in general, resulted in higher K, Zn, and Fe leaf contents and thus can be considered a successful drought stress mitigator in potatoes.

3.3. Antioxidants Enzymatic Activity

A significant increase in the antioxidant enzymatic activities of SOD, POD, CAT, PPO, and APX, along with total protein contents, was recorded in potato leaves under water deficit conditions in comparison with those of well-watered (100 ETc). Regardless of the exogenous application of ZnO-NPs and SiO₂-NPs, a consistent increase in antioxidant enzymatic activity with an increase in water shortage from 100% ETc to 50% ETc was found (Figure 6). Abiotic stresses stimulate signal transduction to produce ROS, but the overaccumulation of ROS in stressed plants may lead to oxidative damage. However, plants have adapted themselves to scavenge ROS by upregulating antioxidants' related gene expression and by ROS-scrounging metabolic pathways [87]. The potato plants respond to abiotic stress through ROS homeostasis and biochemical pathways [88,89]. Under water-deficit conditions, the biochemical response in plants includes the accumulation of ROS and the denaturation of proteins and enzymes, which stimulate antioxidant activity [12]. The potato plant utilizes methods of mitigating the harmful effects of drought stress to protect against ROS damage [90]. Both enzymatic and non-enzymatic defense mechanisms effectively scavenge the ROS generated under water stress [90,91].

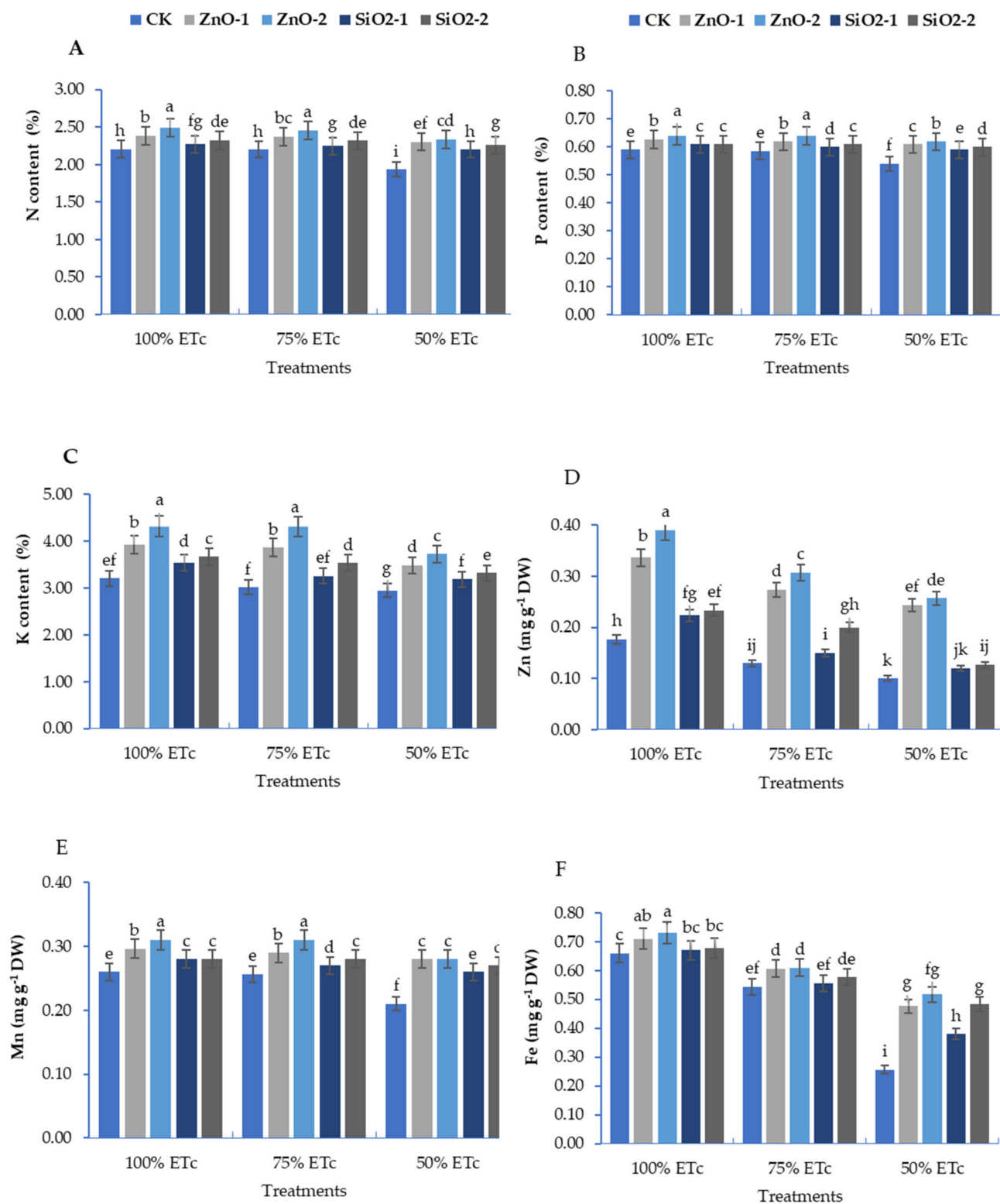


Figure 5. Effect of ZnO and SiO₂ NPs on nitrogen (A), phosphorus (B), potassium (C), zinc (D), manganese (E), and iron (F) of potato plants grown under different water deficit treatments. See Figure 4 for definition of abbreviations.

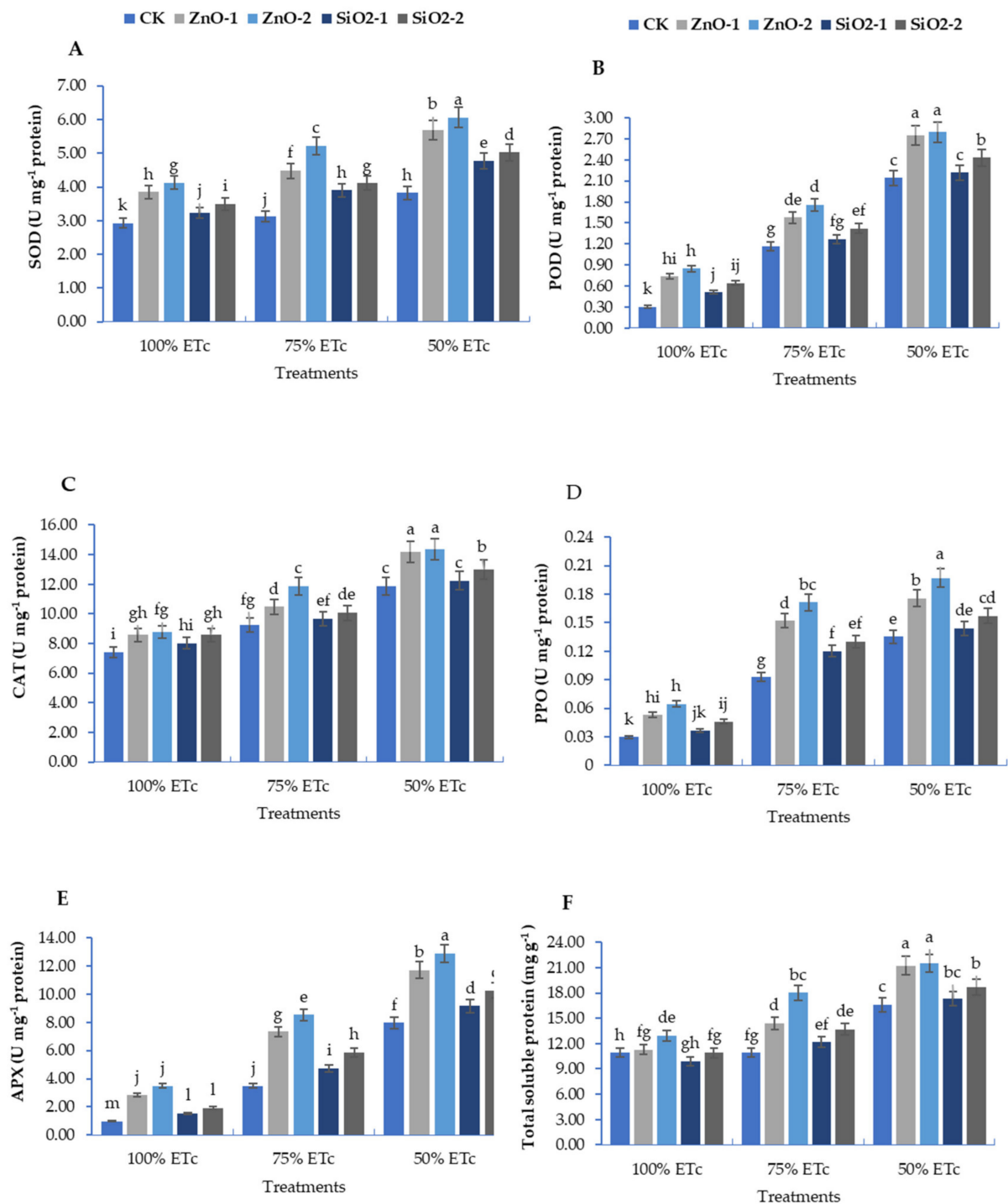


Figure 6. Effect of ZnO and SiO₂ NPs on superoxide dismutase; SOD (A), peroxidase; POD (B), catalase; CAT (C), polyphenoloxidase; PPO (D), ascorbate peroxidase; APX (E), and total soluble protein (F) of potato plants grown under different water deficit treatments. See Figure 4 for definition of abbreviations.

The antioxidant activity of all studied enzymes along with total protein contents showed an increasing pattern in the potato leaves treated with ZnO-NPs and SiO₂-NPs compared with control plants (Figure 6). However, the maximum improvement of these enzymes' activity was noted in plants subjected to ZnO-2 NPs (100 mg L⁻¹) treatment, followed by ZnO-1 NPs (50 mg L⁻¹) and SiO₂-2 NPs (50 mg L⁻¹), respectively. NPs mitigate abiotic stress by increasing the activity of antioxidant enzymes, upregulating specific genes,

and accumulating free nutrients and amino acids [92]. Nanoparticles, due to their nanosize, various regular geometric characteristics, and adverse chemical nature, can efficiently enter plant tissues and may affect enzymatic activities at the cellular level [23]. Moreover, NPs can increase the activity of numerous antioxidant enzymes (i.e., SOD, CAT, APX, POD, and PPO) and thus enhance resistance to environmental stresses in plants [93]. The increase in bioactive compounds is explained partly by the fact that NPs block the transfer of electrons from NADH to ubiquinone, induce oxidative stress, and increase O_2 , H_2O_2 levels, and malondialdehyde (MDA) [66,94,95].

A number of studies reported that ZnO-NPs application significantly lowered oxidative damage and promoted antioxidant activity in plants under abiotic stress [27,96,97]. Thus, the enhanced antioxidant activity and neutralization of ROS in response to ZnO nanoparticles improved subsequent plant growth and development [98]. The adequate supply of ZnO-NPs exhibited increased antioxidant enzymatic and non-enzymatic activities in tomatoes [99], eggplant [28], and lettuce [24]. Sufficient supply of Zn from ZnO nanoparticles under drought stress contributes to genes' up-regulation, enzymatic activation, and protein synthesis, which consequently improve antioxidant defense mechanisms in plants [100]. The increased activity of some antioxidant enzymes in this study can be explained by the fact that NPs can interact with these enzymes to form protein complexes [101]. The increase in CAT and APX activity might result from the fact that ZnO-NPs induce overexpression of the CATa, CATb, and CATc genes, as well as APXa and APXb [102]. Azarin et al. [103] also reported that the APX gene was overexpressed in response to ZnO-NPs exogenous supply.

Under abiotic stress conditions, SiO_2 -NPs play a protective role by enhancing plant water status, ROS scavenging, and enzymatic profiles, which result in the improvement of the defense system by regulating SOD, APX, and CAT activities [104]. Furthermore, SiO_2 -NPs are thought to promote plant growth, support the antioxidant system in times of stress, boost resistance to abiotic stressors, and maintain cell water balance [105,106]. SiO_2 has proven to increase enzyme activities in plants under stress as compared with untreated plants of tomato [75], faba bean [107], and green pea [108]. In salinity-treated potato seedlings, spraying 50 mg L^{-1} SiO_2 -NPs increased the activity of enzymatic antioxidants in comparison with non-treated plants [109].

3.4. Non-Enzymatic Antioxidant Compounds: Total Flavonoids and Phenolic Contents

Non-enzymatic antioxidants such as TFC and TPC were significantly increased under low irrigation treatments, i.e., 75% ETc and 50% ETC, as compared with control (CK) (Figure 7). Under drought stress conditions, plants typically have a ROS protective and antioxidant defense system that reduces oxidative stress by inducing antioxidant enzyme activity and the biosynthesis of phenolic and flavonoid compounds [13,14,110]. Hamouz et al. [111] discovered an increase in TPC and TFC in potatoes grown under extreme temperatures and water shortages. Water shortages increase the *Solanum lycopersicum* plant's TPC [112]. Flavonoids, chemically, are secondary metabolites with antioxidant activity; however, the strength of their activity is determined by the number of free -OH groups in a molecule and their structural position [113]. Phenols, on the other hand, due to their lower electron reduction potential and reactivity as compared with oxygen free radicals, are excellent ROS scavengers [114,115]. Many plants accumulate phenolic compounds because of their beneficial role in alleviating the negative effects of oxidative stress and detoxifying ROS under abiotic and biotic stresses [17]. In the current study, regardless of the stress condition, the application of ZnO-NPs and SiO_2 -NPs significantly increased the contents of TFC and TPC. The application of 100 mg L^{-1} of ZnO-NPs improved these compounds in potato plants grown under water deficit treatments, followed by 50 mg L^{-1} of ZnO-NPs and 50 mg L^{-1} of SiO_2 -NPs, respectively. Plants treated with ZnO-NPs under stress conditions have shown the highest flavonoids and phenolic contents [116]. The increase in TFC and TPC compounds in this study coincides with Ghani et al. [18], who observed that applications of 100 mg L^{-1} SiO_2 -NPs promoted a rise in these compounds in cucumber.

Similar findings were also reported in tomatoes under drought stress [117]. When plants are exposed to NPs, they tend to increase the production of antioxidant compounds such as phenolic and flavonoid compounds [116]. Furthermore, both flavonoids and phenols eliminate ROS, prevent lipid peroxidation of cellular membranes, and maintain cell membrane fluidity and normal functionality in plants under various abiotic stresses [118].

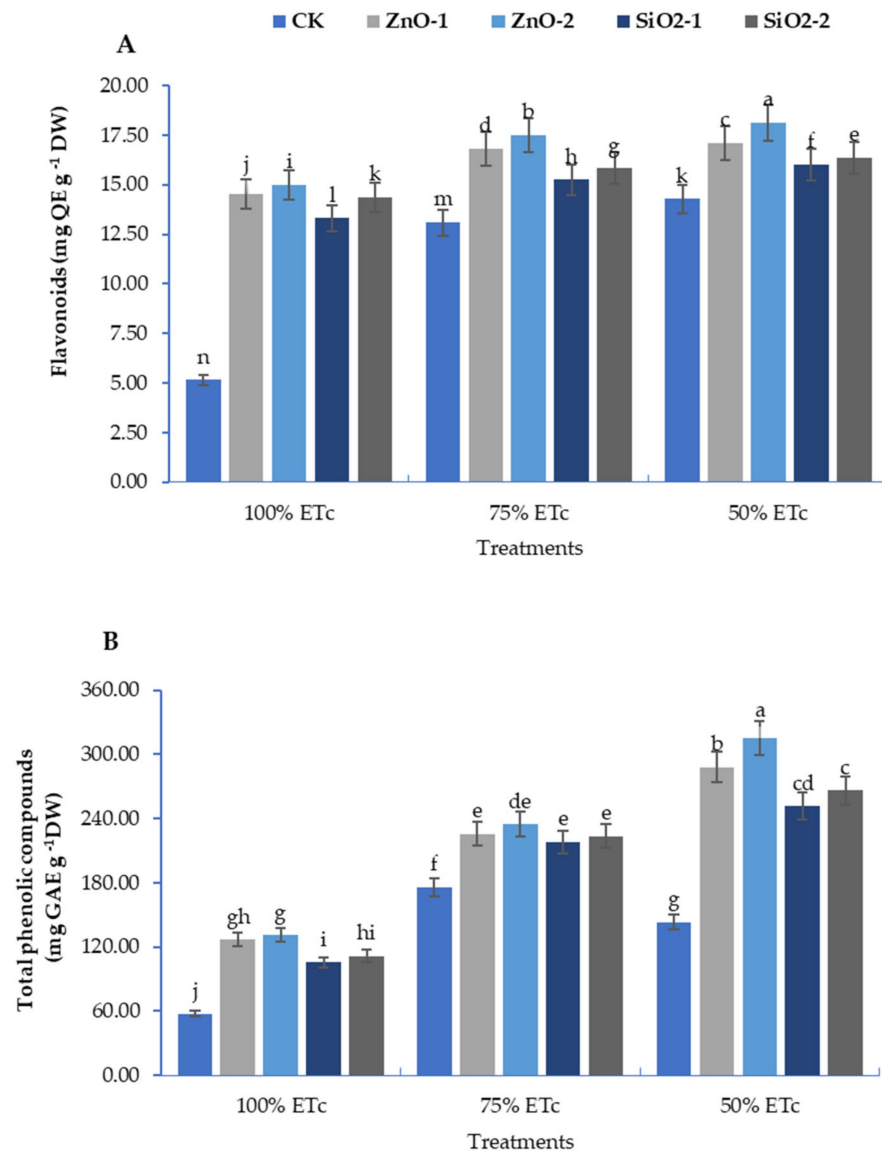


Figure 7. Effect of ZnO and SiO₂ NPs on flavonoids (A); and total phenolic compounds (B) of potato plants grown under different water deficit treatments. See Figure 4 for definition of abbreviations.

3.5. Oxidative Stress Biomarkers (MDA) and (H₂O₂)

Both MDA and H₂O₂ content significantly increased under water shortages (Figure 8A,B). The highest contents of these compounds were observed in 50% ETc, and the lowest content was found under 100% ETc treatment (Control). In water-stressed potato plants, MDA and H₂O₂ levels increased as compared with well-watered plants [119]. Water stress has been shown to increase MDA content in tomato plants, which may be due to ROS accumulation, increased lipid peroxidation, and thus membrane damage [120,121]. Severe drought results in ROS accumulation and subsequent oxidative stress in plants [122,123]. In general, ROS accumulation under drought stress leads to the overproduction of MDA and H₂O₂, which impair cell membrane structure and functionality and, therefore, can be used as biomarkers to identify oxidative stress intensity [124]. It has been shown that ZnO-NPs

(50 and 100 ppm) and SiO₂-NPs (25 and 50 ppm) foliar application significantly reduced MDA and H₂O₂ content under water shortage treatments; however, foliar application of ZnO-NPs at 100 mgL⁻¹ stood out as the most effective as compared with all other treatments, especially under 50% ETc stress (Figure 8A,B). Ghani et al. [18] reported that ZnO-NPs treatment favored *Cucumis sativus* growth under drought stress by significantly reducing the hyperaccumulation of H₂O₂ and MDA. Moreover, the ZnO-NPs application as a foliar spray in tomato plants under water deficit conditions (75, 50, and 25% FC) resulted in reduced MDA and H₂O₂ contents in leaves [69]. Similar findings were also noted in *Zea mays* under drought stress, where the leaves treated with ZnO-NPs resulted in well-maintained plasma membrane stability due to reduced H₂O₂ and MDA accumulation and lipid peroxidation [30]. Spraying SiO₂-NPs on strawberries under drought stress increased SOD, APX, and CAT antioxidant activity and decreased MDA and H₂O₂ content [125]. Likewise, spraying pea plants with SiO₂-NPs mitigated the negative effects of drought stress by reducing MDA and H₂O₂ contents [108]. The application of NPs increases the activity of SOD, CAT, APX, and POD enzymes and reduces H₂O₂ and MDA levels by regulating glutathione reductase (GSH) and ascorbate (ASC) levels [126,127].

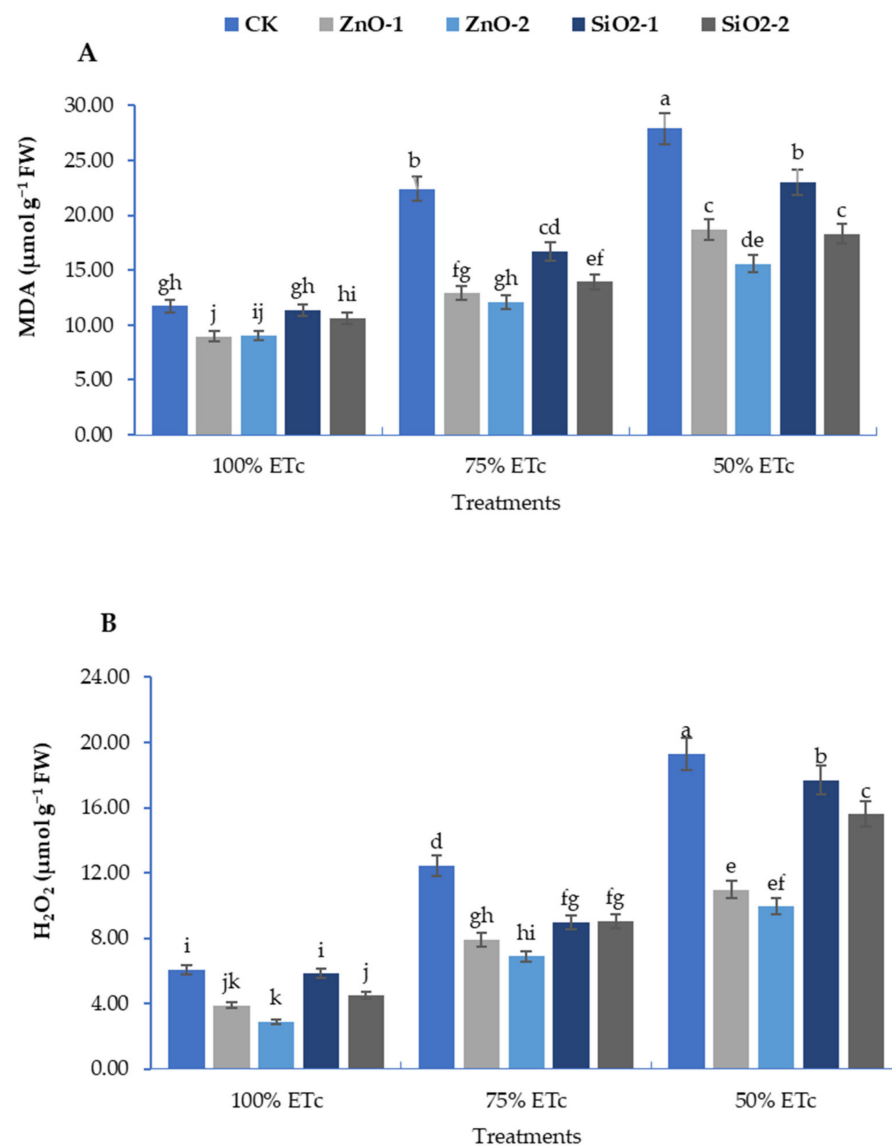


Figure 8. Effect of ZnO and SiO₂ NPs on malondialdehyde; MDA (A), and hydrogen peroxide; H₂O₂ (B), Flavonoids of potato plants grown under different water deficit treatments. See Figure 4 for definition of abbreviations.

3.6. Correlation Study

The PCA (Figure 9) and Pearson's correlation (Figure 10) were performed to understand the relationships among the studied traits of potato plants grown under different treatments of water stress and nanoparticles. Both PCA and Pearson's correlations revealed that changes in the morphological and biochemical traits of water-stressed potato plants were passively correlated. Two-dimensional PCA was utilized to assimilate 22 indexes of water-stressed potato plants treated with ZnO and SiO₂ nanoparticles. The results showed that the first two components (F1, F2) were the most influential and accounted for 92.82% of the total variance. For example, F1 and F2 contributed 59.69% and 33.13% of the variance in the dataset, respectively. F1 had a significant positive influence on growth traits, mineral uptake, and TFC, whereas F2 had a significant positive influence on the SOD, POD, CAT, PPO, APX, TPC, MDA, and H₂O₂.

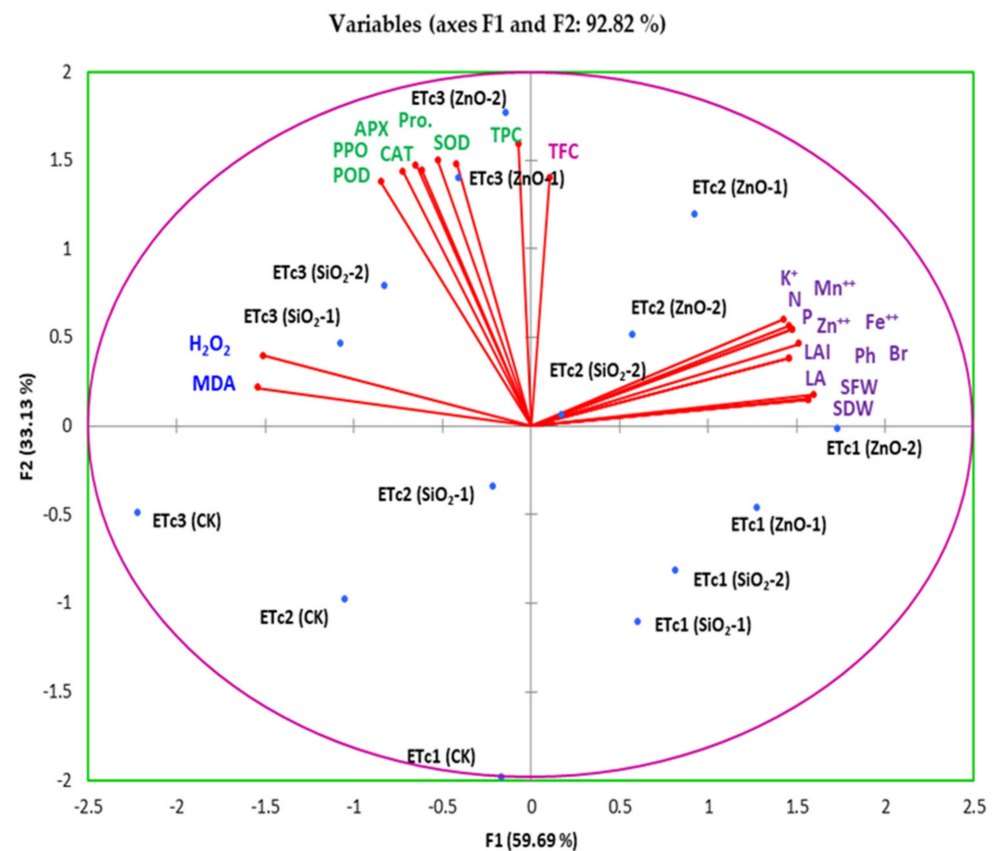


Figure 9. Principal component analysis of morpho-biochemical traits of potato plants grown under water stress and nanoparticle treatments.

Pearson's correlation analysis expressed in Figure 10 showed significant correlations (bold numbers) and non-significant correlations (non-bold numbers) among various morphological, mineral, and antioxidant traits. Briefly, morphological traits were significantly and positively correlated with minerals, and they were negatively correlated with MDA and H₂O₂. These results indicate that the ZnO-NPs and SiO₂-NPs foliar applications were effective in mitigating the effects of water shortage damage through the improvement of essential nutrient uptake and modulating antioxidant enzymes. Such changes might lead to an enhancement of plant tolerance to drought stress, which improves potato growth and productivity. It has been reported that ZnO and SiO₂ NPs significantly mitigated water deficit stress and enhanced potato productivity [39,128].

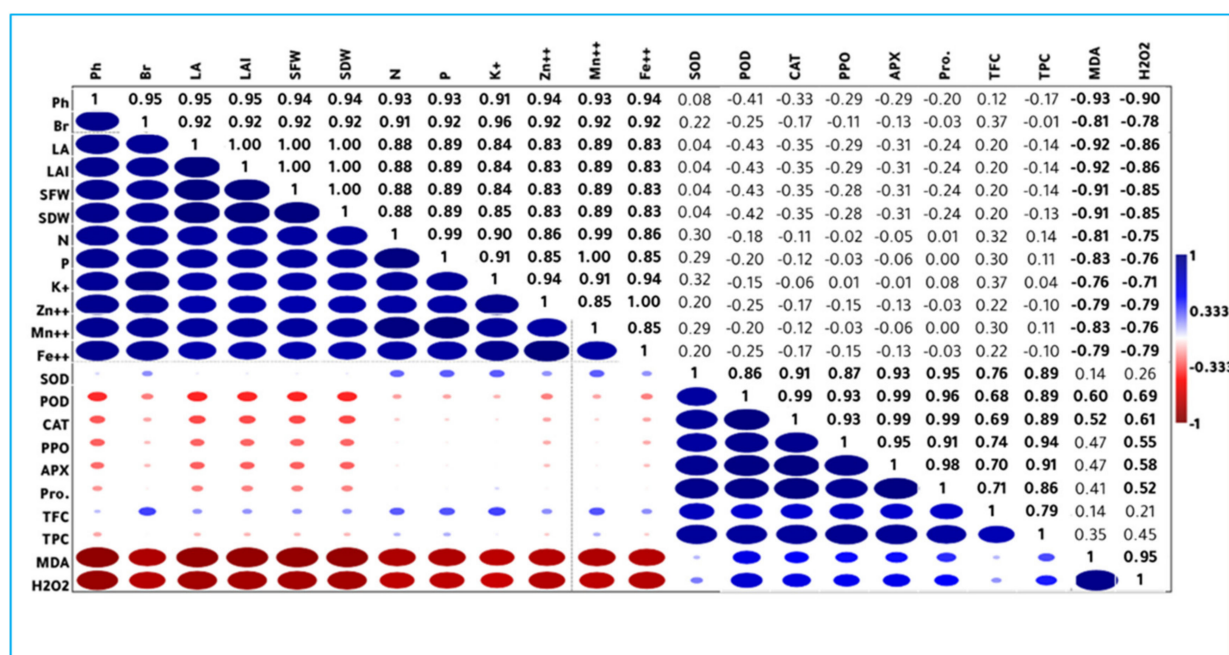


Figure 10. The correlation between different morpho-biochemical traits of potato plants grown under water stress and nanoparticle treatments.

4. Conclusions

The foliar application of ZnO-NPs and SiO₂-NPs positively enhanced the mineral uptake as well as the morphological, growth, and physiological traits of potato plants grown under water shortage conditions. However, the application of ZnO NPs at 100 mg L⁻¹ resulted in the highest values for most of the potato plant traits that were grown under different water deficit stress treatments in comparison with other treatments. The enhanced antioxidant activity and neutralization of ROS in response to ZnO nanoparticles improved subsequent plant growth and development. The morphological traits were significantly and positively correlated with minerals and were negatively correlated with MDA and H₂O₂. These results indicate that the ZnO-NPs and SiO₂-NPs foliar applications were effective in mitigating the effects of water shortage stress through the improvement of essential nutrient uptake and modulating antioxidant enzymes. Such changes might lead to improvements in plant tolerance to water stress, which can improve potato growth and productivity.

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