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# Drought Stress Amelioration in Sesame Cultivars: Unraveling the Combined Potential of $MnSO_4$ Seed Treatment and Foliar Nutrition

**Ghasem Najafi, Mohammad Javad Zarea*, Arash Fazeli, Batool Zarei**

*Department of Agronomy and Crop Breeding, Faculty of Agriculture, Ilam University, Ilam, Iran*

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## ABSTRACT

Water scarcity is a critical factor that restricts crop production, and projections indicate that its severity will escalate in the future due to the impacts of global warming. The objective of this research was to assess the role of $MnSO_4$ in improving water deficit tolerance in two sesame cultivars, Dashtestan2 and Naz Takshakheh. A factorial pot study was conducted based on randomized complete block design with three replications at the Research Greenhouse of the Faculty of Agriculture, University of Ilam in 2019. $MnSO_4•7H_2O$ was utilized via seed priming, foliar application, or a combination of both methods. Three different water level regimes were established: 75% field capacity (FC) representing well-watered conditions, 50% FC indicating mild water stress, and 25% FC denoting severe water stress. The results of experiment indicated that cultivar Dashtestan2 produced a greater seed yield compared to the Naz Takshakheh cultivar, under both well-watered and water-deficient conditions. Foliar application was more effective than seed priming in promoting proline accumulation and enhancing the activities of catalase and ascorbate peroxidase enzymes. Plants treated with both seed priming and foliar application with $MnSO_4•7H_2O$ demonstrated enhanced antioxidant enzyme activity and higher seed yield. Based on the results, the application of manganese sulfate through seed priming, foliar application, and a combination of both techniques led to a notable increase in seed yield for both sesame cultivars facing water deficit stress. The Dashtestan2 cultivar showed especially significant improvements in seed yield, which can be attributed to increased activity of antioxidant enzymes and osmotic regulators. Among the various methods for applying manganese sulfate, the combination of seed priming and foliar spraying demonstrated superior effectiveness in enhancing tolerance to water deficit stress.

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## 1. Introduction

Sesame (*Sesamum indicum* L.) is a vital oilseed valued for its various industrial, pharmaceutical, and nutritional uses (Kermani *et al*., 2019; Hussain *et al*., 2023). The seeds are rich in protein, oil, and natural antioxidants such as sesamin, sesamolin, and tocopherol (Balouchi *et al*., 2023). Sesame is typically cultivated in arid and semi-arid regions worldwide. Plants are exposed to various environmental stresses during growth and development under natural and agricultural conditions. Among these, drought is one of the most severe environmental stresses that severely affects crop growth and productivity, especially in arid and semi-arid regions such as Iran, where annual average rainfall is about 250 mm (Hamarash *et al*., 2022). Drought stress disrupts growth by causing various morphological, physiological, biochemical, and molecular changes, which ultimately affect the crop's final yield (Rasheed and Malik, 2022). The response of plants to drought stress depends on growth stage, species, the severity and duration of the drought (Gray and Brady, 2016). Water deficiency reduces photosynthesis by reducing leaf area index, stomata conductance, and photosynthetic pigments concentration. Under water-deficient conditions, plant growth and yield are reduced due to the limited production of photosynthetic materials (Dawood *et al*., 2019). Water deficiency, the most limiting stress in agriculture, can severely impact both seed quality and yield. Therefore, investigating how plants cope with

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* Corresponding author.
E-mail address: zareamj@yahoo.com

water limitation is highly valuable and should be prioritized in the near future, particularly in arid and semi-arid environments such as Iran (Sobhanian *et al.*, 2020). Plants respond to water deficiency by increasing the activity of antioxidant defense systems to eliminate reactive oxygen free radicals (Kar, 2011) and accumulating organic osmolytes to maintain osmotic balance (Blum, 2017). When plants experience drought stress, they activate a range of antioxidant defenses to mitigate the harmful effects of oxidative stress. These include enzymes like catalase (CAT), superoxide dismutase (SOD), peroxidase (POX), ascorbate peroxidase (APX), and non-enzymatic antioxidants like glutathione and ascorbate (Chen *et al.*, 2016).

Compatible compounds such as proline, glycine betaine or polyamines, as well as sugars, are produced as osmotic protectors in plants during stress conditions (Hasanuzzaman *et al.*, 2019). Most plants respond to stress conditions such as drought, salinity, nutrient deficiency, and high temperatures by increasing proline levels (Jogawat, 2019). Since proline is an important osmotic regulator, the accumulation of proline increases resistance to water deficiency in plants (Su *et al.*, 2018). Glycine betaine, along with other osmotic regulators, is commonly accumulated in plants during stress conditions (Hernandez-Leon and Valenzuela-Soto, 2023). Many strategies exist to enhance the growth and development of plant species under both stress and non-stress conditions. One effective approach is seed priming, a chemical treatment applied before sowing. This method promotes early seedling emergence and accelerates the emergence rate, even in extreme weather conditions (Ghosh *et al.*, 2023). During priming, seeds are soaked in water or in various solutions, including organic and inorganic salts, within a controlled environment. After soaking, the seeds are dried before sowing. This process helps regulate germination by managing the moisture and temperature of the seeds (Diya *et al.*, 2024). Priming allows seeds to absorb sufficient water for germination using less moisture than is usually required for natural germination (Farooq *et al.*, 2019). Many organic and mineral substances, hormones, and plant extracts have proven effective as priming agents in various crops against abiotic stresses, including drought and salinity stresses (Amritha *et al.*, 2021). Manganese sulfate is a key basic manganese salt, accounting for nearly 80% of the world's manganese products, which are produced using either manganese sulfate or manganese sulfate solutions. Additionally, manganese sulfate has numerous applications in both industry and agriculture (Li *et al.*, 2023). Priming maize seeds with a $MnSO_4$ solution enhanced growth, grain manganese content, and seed yield. Moreover, increasing the concentration of the priming solution to 0.2% $MnSO_4$ for 12 hours resulted in a linear increase in both seed yield and grain manganese content (Muhammad *et al.*, 2015).

This study aims to investigate the efficacy of manganese sulfate ($MnSO_4{\bullet}7H_2O$) in enhancing drought tolerance in two sesame cultivars (Dashtestan2 and Naz Takshakheh) under varying water deficit conditions. Specifically, the research evaluates the impact of different application methods (seed priming, foliar spraying, and their combination) on antioxidant enzyme activity (CAT and APX), proline accumulation, and seed yield at three irrigation levels (75%, 50%, and 25% of field capacity). Additionally, the study compares cultivar-specific responses to water stress and identifies the most effective $MnSO_4$ application strategy for mitigating drought-induced yield losses. The findings will provide critical insights into optimizing sesame production under water-scarce conditions, contributing to sustainable agriculture in arid and semi-arid regions.

## 2. Materials and methods

A factorial experiment was carried out based on randomized complete block design with three replications to assess the impact of seed priming and foliar application of $MnSO_4{\bullet}7H_2O$ on the growth and yield of sesame under water deficiency conditions. The research was conducted at the greenhouse of the Faculty of Agriculture, the University of Ilam, in December 2019 (min and max temperatures averaged 24°C and 34°C, respectively). Three experimental factors were used including two sesame cultivars (Dashtestan2 and Naz Takshakheh), different application types including seed priming (unprimed seeds and seed primed) and foliar application (control and treated), and the third factor including three level of water stress (well-watered (75% FC), mild water deficiency (50% FC) and severe water deficiency (25% FC). Seeds from two sesame varieties, Dashtestan2 and Naz Takshakheh, were acquired from the Seed and Plant Improvement Institute located in Karaj, Iran (Table 1).

**Table 1. Properties of the studied cultivars**

| Cultivars | Branching | Seed color | 1000 seed weight (g) | Response to water deficiency | Plant height (cm) |
|---|---|---|---|---|---|
| Dashtestan2 | Several branches | Light brown | 4 | Tolerant | 142-145 |
| Naz TakShaskheh | Single branches | Cream | 2.6-2.9 | Sensitive | 100-120 |

The experimental units consisted of 72 plastic pots, each with dimensions of 25 cm in diameter and height, filled with 7 kg of field soil. To ensure proper drainage, four holes were drilled at the bottom of each pot, and equal-weight pebbles were added to all of them. Before planting, the soil's texture, pH, and electrical conductivity (EC) were measured at the soil laboratory at Ilam University. Following the soil analysis, fertilizers including phosphorus (triple superphosphate), nitrogen (urea), and potash fertilizers were incorporated into the soil in the pots (Table 2).

**Table 2. Soil physicochemical properties**

| Texture | E.C. (dS $m^{-1}$) | pH | O.C. | N | Mn | P | K |
|---|---|---|---|---|---|---|---|
| | | | (%) | | ($mg\ kg^{-1}$) | | |
| Clay loam | 0.3 | 7 | 1.2 | 0.12 | 0.08 | 8.5 | 420 |

The process of disinfecting seeds prior to planting consisted of multiple stages. Initially, the seeds were treated with 70% ethanol for a duration of 30 seconds, then immersed in a 5% sodium hypochlorite solution for five minutes. The seeds were then thoroughly washed multiple times with distilled water to eliminate any remaining sodium hypochlorite. Ten seeds were planted in each pot at a depth of 1 cm. After germination, five plants were retained in each pot. Sesame plant growth was carried out in a greenhouse with average day and night temperatures of 34°C and 24°C, respectively, relative humidity of 45-60%, and a light period of 16 hours. Pots were regularly irrigated prior to the onset of the water deficiency treatment to maintain soil moisture at 75% of FC, which is 40% for this soil type. Irrigation treatments began one month after plant emergence. The weights of each pot for the three treatments—75%, 50%, and 25% FC were determined to be 1.10 kg, 9.4 kg, and 8.7 kg, respectively. A pot weighing system was used to determine irrigation time, and irrigation was performed when the pot weight for each treatment reached a predetermined amount based on the field capacity.

A concentration of 0.3% manganese sulfate was used for priming the seeds of both sesame cultivars. Thus, the seeds of both sesame cultivars were immersed in distilled water (as the control) and manganese sulfate solution at a ratio of 1:5 (one gram of seed in 5 milliliters of solution) for seven hours. Afterward, the seeds were placed on filter paper to achieve the initial moisture level. Foliar spraying of $MnSO_4 \bullet 7H_2O$ was applied twice: 48 hours before exposure to water deficiency and 7 days after the onset of water stress. For foliar spraying of manganese sulfate, manganese sulfate was used at a concentration of 0.3% for the Dashtestan2 and Naz Takshakheh cultivars. Foliar spraying was done using a 2-liter sprayer. Foliar spraying was conducted in a way that covered the entire leaf surface of the plant. Control treatments were sprayed using distilled water. Leaf sampling was conducted 48 hours after the second foliar spray at 10 AM, the third fresh leaf of each plant was harvested and stored at -80°C for measurement of biochemical indicators, including activities of CAT, POX, APX, as well as the concentrations of proline, soluble sugar, and soluble protein. To evaluate seed yield, sampling was performed at the maturity stage.

CAT enzyme activity was measured using the method of Aebi (1984). In order to measure the CAT enzyme activity, first, the spectrophotometer was set to a wavelength of 240 nm. Then the microtubes containing the extracted enzyme were taken out of the refrigerator and placed on ice. Then 3000 µl of 100 mM phosphate buffer and 40 µl of 30 mM hydrogen peroxide were poured into a quartz cell. The cell containing these two substances was placed in the spectrophotometer and used to calibrate the device. Next, 100 µl of enzyme extract was added to it and after five minutes of starting the reaction at room temperature, absorption was performed using a spectrophotometer at a wavelength of 240 nm. The method of MacAdam et al. (1992) was used to measure POX enzyme activity. To measure the activity of the POX enzyme, first, the spectrophotometer was set to a wavelength of 470 nm. Then the microtubes containing the extracted enzyme were taken out of the refrigerator and placed on ice. Then, 3 ml of 100 mM phosphate buffer, 50 µl of 200 mM guaiacol, and 40 µl of 30 mM hydrogen peroxide were mixed. Then 100 µl of enzyme extract was added to each sample and five minutes after the start of the reaction at laboratory temperature, absorption was performed at a wavelength of 470 nm using a spectrophotometer. The activity of the POX enzyme was expressed as enzyme units per gram of fresh weight (FW). APX enzyme activity was measured by the method of Nakano and Asada (1987). The reaction mixture consisted of 1500 µl of 50 mM phosphate buffer (pH 7.8), 400 µl of 0.1 mM hydrogen peroxide, 400 µl of 30% ascorbic acid, 600 µl of 0.1 mM EDTA, and 100 µl of enzyme extract. APX enzyme activity was calculated based on the rate of hydrogen peroxide decomposition per minute per mg of protein at a wavelength of 290 nm and using an extinction coefficient of 2.8 $mM^{-1}cm^{-1}$. In order to calculate seed yield, all plants in each pot (5 plants) were harvested 100 and 105 days after planting in the Naz Takshakheh and Dashtestan2 cultivars, respectively, and after separating the seed from the plants, the seed yield per plant was calculated. Before conducting the statistical analysis of the data and analysis of variance, normal distribution tests for the data and errors were performed using the Kolmogorov, Immonrov, and Levin methods with SPSS software. The comparison of main effects means was conducted using Duncan's multiple range method at a probability level of 5% with MSTATC software.

## 3. Results and discussion

The analysis of variance showed that the individual effects of cultivar, spray, Seed Priming and water deficiency on the examined traits were statistically significant ($p \leq 0.01$) (Table 3).

**Table 3. Analysis of variance of traits of two sesame plant cultivars in response to manganese sulfate application methods under water deficiency**

| S.O.V. | df | Mean Squares | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | Seed yield per plant | Proline | Soluble sugar content | Soluble protein content | CAT activity | POX activity | APX activity |
| Replication | 2 | $0.00015^{ns}$ | $0.00041^{ns}$ | $0.00011^{ns}$ | $0.0016^{ns}$ | $0.00066^{ns}$ | $0.00002^{ns}$ | $0.000031^{ns}$ |
| Cultivar (C) | 1 | $0.195^{**}$ | $0.00097^{*}$ | $0.00087^{**}$ | $0.471^{**}$ | $0.0224^{**}$ | $0.0074^{*}$ | $0.144^{**}$ |
| Spray (S) | 1 | $0.53^{**}$ | $0.156^{**}$ | $0.512^{**}$ | $0.4036^{**}$ | $0.278^{**}$ | $0.307^{**}$ | $0.45^{**}$ |
| Priming (P) | 1 | $0.127^{**}$ | $0.046^{**}$ | $0.168^{**}$ | $0.1092^{**}$ | $0.15^{**}$ | $0.115^{**}$ | $0.18^{**}$ |
| Water deficiency (W) | 2 | $0.634^{**}$ | $0.452^{**}$ | $0.15^{**}$ | $0.4368^{**}$ | $0.608^{**}$ | $0.165^{**}$ | $0.496^{**}$ |
| C × S | 1 | $0.052^{**}$ | $0.000015^{ns}$ | $0.00056^{*}$ | $0.00044^{ns}$ | $0.0004^{ns}$ | $0.0012^{**}$ | $0.0095^{ns}$ |
| C × P | 1 | $0.008^{**}$ | $0.0000023^{ns}$ | $0.0014^{**}$ | $0.007^{*}$ | $0.00015^{ns}$ | $0.00035^{**}$ | $0.0034^{ns}$ |
| C × W | 2 | $0.0014^{**}$ | $0.00000019^{ns}$ | $0.0014^{**}$ | $0.0366^{**}$ | $0.000006^{ns}$ | $0.00023^{**}$ | $0.00074^{**}$ |
| S × P | 1 | $0.0052^{**}$ | $0.000044^{ns}$ | $0.043^{**}$ | $0.000015^{ns}$ | $0.0098^{**}$ | $0.000034^{ns}$ | $0.0295^{**}$ |
| S × W | 2 | $0.00036^{ns}$ | $0.0067^{**}$ | $0.00008^{ns}$ | $0.0148^{**}$ | $0.0101^{**}$ | $0.0015^{**}$ | $0.0737^{**}$ |
| P × W | 2 | $0.005^{**}$ | $0.0017^{**}$ | $0.0002^{ns}$ | $0.0156^{**}$ | $0.0054^{**}$ | $0.00091^{**}$ | $0.0299^{**}$ |
| C × S ×P | 1 | $0.0042^{**}$ | $0.0000023^{ns}$ | $0.011^{**}$ | $0.00029^{ns}$ | $0.000063^{ns}$ | $0.00034^{**}$ | $0.0018^{ns}$ |
| C × S × W | 2 | $0.0006^{*}$ | $0.0000083^{ns}$ | $0.00009^{ns}$ | $0.00069^{ns}$ | $0.00047^{ns}$ | $0.0007^{**}$ | $0.0027^{ns}$ |
| C × P × W | 2 | $0.0024^{**}$ | $0.000014^{ns}$ | $0.0002^{ns}$ | $0.00064^{ns}$ | $0.0025^{ns}$ | $0.00034^{**}$ | $0.0009^{ns}$ |
| S × P × W | 2 | $0.0045^{**}$ | $0.000056^{ns}$ | $0.0005^{**}$ | $0.002^{ns}$ | $0.0182^{**}$ | $0.00084^{**}$ | $0.0024^{ns}$ |
| C × S × P × W | 2 | $0.0047^{**}$ | $0.000025^{ns}$ | $0.00012^{**}$ | $0.0015^{ns}$ | $0.0027^{ns}$ | $0.00067^{**}$ | $0.00051^{ns}$ |
| Error | 46 | 0.0001 | 0.00021 | 0.00008 | 0.0011 | 0.00088 | 0.000038 | 0.0035 |
| C.V. (%) | | 2.39 | 3.76 | 1.51 | 8.28 | 4.23 | 1.15 | 18.31 |

### *3.1. Seed yield per plant*

The mean comparison indicated that the seed yield of both sesame cultivars was adversely affected by rising water deficiency levels. The reduction in seed yield can be attributed to the negative effect of drought stress on the seed number per plant and the weight of 1000 seeds, which was linked to a shortened duration of the seed filling process (Alizadeh *et al.*, 2010). The seed yield of Dashtestan2 and Naz Takshakheh cultivars decreased from 0.568 grams and 0.526 grams, respectively, under well-watered conditions (75% FC) to 0.241 grams and 0.218 grams per plant under severe drought conditions (25% of FC) (Fig. 1).

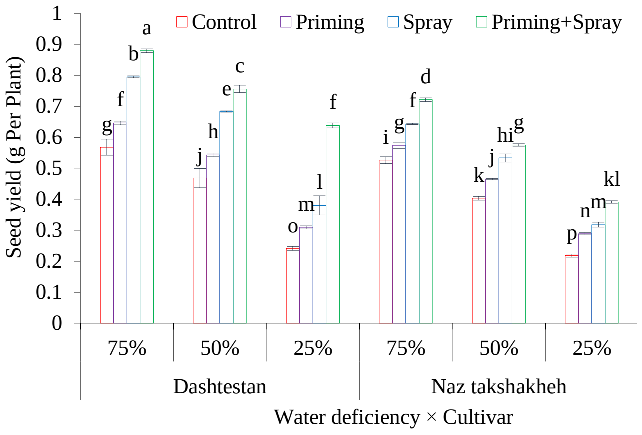

**Figure 1. The effect of different manganese sulfate applications on seed yield of two sesame cultivars under water-deficient conditions. Different letters indicate significant differences (p<0.05, Duncan's test).**

The most noticeable impact of water deficiency on plants is the decrease in leaf growth and development, caused by slowed growth and cell division. This reduction subsequently leads to lower dry matter accumulation and crop yield. Additionally, a study showed that different soybean genotypes experienced a significant reduction in seed yield under water-deficient conditions (Soliman *et al*., 2025). At all levels of water deficiency, seed yield was higher in the Dashtestan2 cultivar than in the Naz Takshakheh cultivar. Priming seeds with nutrients enhances plant establishment, accelerates phenological development, boosts yield, and improves the micronutrient concentration in crops. Additionally, in many instances, priming seeds with micronutrients can decrease the requirement for these nutrients and reduce dependence on fertilizers. Seed priming is a straightforward and cost-effective technique for nutrient application (Farooq *et al*., 2012).

The findings indicated that utilizing manganese sulfate through a combination of seed priming and solution spraying proved to be more effective in mitigating the impact of water scarcity on seed yield than employing each method independently. The highest seed yield, 0.879 g plant$^{-1}$, was obtained from the Dashtestan2 cultivar under well-watered conditions (75% FC) using the seed priming and solution spraying treatment. In contrast, the lowest seed yield, 0.218 g/plant, was recorded for the Naz Takshakheh cultivar under severe water deficiency conditions (25% FC) without any treatment (control) (Fig. 1). The results of this study showed that the application of manganese sulfate in the form of seed priming, foliar spraying, and seed priming + solution spraying significantly and remarkablyincreased the seed yield per plant of both sesame cultivars at all levels of drought stress. The enhancement in seed yield from the application of iron, zinc, and manganese can be linked to these elements' ability to boost the activity of antioxidant enzymes, including SOD, CAT, and POX, which help mitigate ROS (Waraich *et al*., 2012).

Furthermore, another study found that foliar spraying of micronutrients led to improved wheat yield and its components (Shoormij *et al*., 2022). Other research results showed that yield and yield components in different canola cultivars decreased under late-season drought stress (Khayat Moghadam *et al*., 2021). Under water-deficient stress conditions, the application of zinc and manganese through foliar treatments on canola (Khodabin *et al*., 2022) and safflower (Movahhedy-Dehnavy *et al*., 2009) resulted in increased seed yield.

### *3.2. Proline content*

The research results showed that as the levels of water deficiency escalated, there was a corresponding increase in the proline concentration found in sesame leaves. Specifically, proline levels increased from 0.224 mg/g of leaf FW under well-watered conditions (75% of FC) to 0.473 mg/g of leaf FW at the severe water deficiency level (25% of FC) (Fig. 2). Under water deficiency stress conditions, plants accumulate organic osmolytes to maintain osmotic balance (Blum, 2017). A high concentration of osmoprotectants, including proline, sugars, polyamines, and glycine betaine, is generally associated with increased biosynthesis and improved stress tolerance in plants (Kaur *et al*., 2017). Proline serves a dual function: at low to moderate concentrations, it has beneficial effects and plays a role in signaling, while at higher concentrations, it can be toxic to living cells. Beyond osmotic regulation, osmoprotectants also perform various other functions, including scavenging free radicals (Szabados and Savouré, 2010), inducing the expression of osmotic stress-related genes, and stabilizing cell membranes and proteins (Theocharis *et al*., 2012). Many studies have indicated an increase in proline levels due to water deficiency stress in various plants, including wheat (Kamruzzaman *et al*., 2023), rapeseed (Farahani *et al*., 2020), sorghum (Amoah and Antwi-Berko, 2020), and chickpea (Seifikalhor *et al*., 2022).

Comparisons of the mean data indicated that the foliar application of manganese sulfate increased proline levels in sesame plants at all levels of water deficiency. Proline concentration increased by 0.085, 0.065, and 0.13 mg/g of leaf FW at 75%, 50%, and 25% of FC, respectively, compared to the control treatment (no foliar application) (Fig. 2). Overall, these results indicate that the foliar application of manganese sulfate enhances drought tolerance. Several studies have linked the increase in proline levels from foliar applications of zinc and manganese to the activation of protein-degrading enzymes, which convert proteins into the amino acid proline (Babaeian *et al*., 2011; Waraich *et al*., 2012).

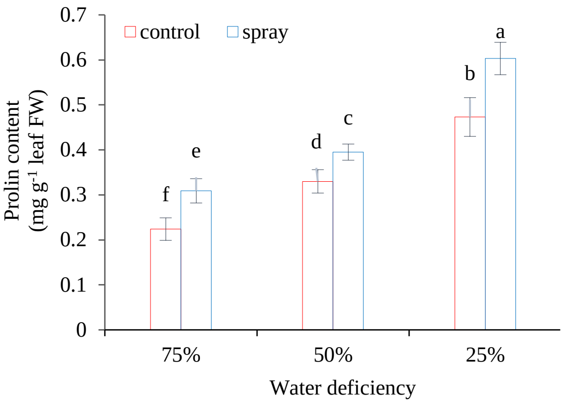

**Figure 2. The effect of foliar spraying with manganese sulfate on proline content in sesame leaves under water deficiency conditions. Different letters indicate significant differences (p<0.05, Duncan's test).**

Proline concentration in sesame leaves increased with seed priming under all levels of water deficiency. Priming sesame seeds with manganese sulfate led to a more significant rise in proline levels at all three levels of water deficiency compared to the control condition without priming. Specifically, seed priming led to increases in proline of 0.048, 0.036, and 0.069 mg $g^{-1}$ of FW at 75%, 50%, and 25% of FC, respectively, compared to the control (Fig. 3). Proline accumulation under water deficit conditions functions as an osmolyte and enhances the ability to repair damage (Kumar *et al*., 2011; Anjum *et al*., 2011). Water deficit stress results in increased proline accumulation in wheat (Sawhney and Singh, 2002) and soybean (Krüger, 2002). Additionally, manganese application has been reported to increase proline content in wheat leaves subjected to drought stress (Ahmad *et al*., 2019).

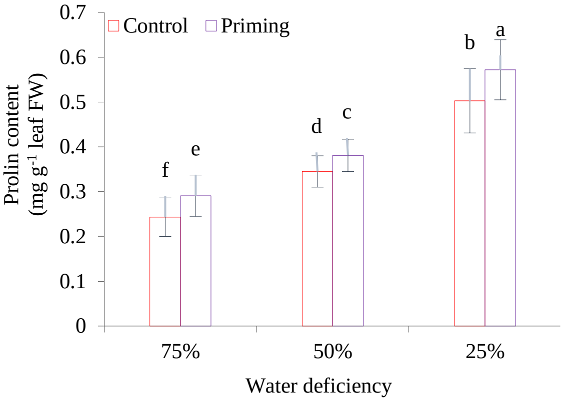

**Figure 3. The effect of seed priming with manganese sulfate on leaf proline content under water deficiency conditions. Different letters indicate significant differences (p<0.05, Duncan's test).**

### *3.3. Soluble sugar*

Increasing water deficiency intensity elevated the soluble sugar content in both sesame cultivars. In the Dashtestan2 and Naz Takshakheh cultivars, the soluble sugar content increased from 0.406 and 0.374 mg $g^{-1}$ leaf dry weight (DW) under well-watered conditions to 0.478 and 0.448 mg $g^{-1}$ leaf DW at mild water deficiency (50% FC), respectively, reaching 0.568 and 0.543 mg $g^{-1}$ leaf DW under severe water deficiency (25% FC) conditions (Fig. 4). Other studies have found that drought stress conditions increase the levels of soluble sugars in various plants, including corn (Zi *et al*., 2022), rice (Wang *et al*., 2019), wheat (Johari-Pireivatlou, 2010), rapeseed (Moradshahi *et al*., 2004), and soybean (Du *et al*., 2020). The activity of the alpha-amylase enzyme seems to increase under water deficiency stress, resulting in a higher concentration of soluble sugars due to starch hydrolysis (Setter *et al*., 2001). During periods of water deficiency, the carbohydrate content in the plant rises, mainly serving functions in osmotic regulation, protection, and carbon storage (Cechin *et al*., 2006). These sugars act as a defense mechanism during water deficiency stress, helping to maintain elevated turgor pressure within the cells (Kishor *et al*., 2005).

Increasing water deficiency stress and employing various methods of manganese sulfate application—such as seed priming, foliar spraying, and a combination of both—resulted in a higher concentration of soluble sugars in the leaves of both sesame cultivars across all three levels of water deficiency stress compared to the control treatment (which did not receive manganese sulfate treatment). The Dashtestan2 cultivar demonstrated the highest concentration of soluble sugar, measuring 0.838 mg $g^{-1}$ dry leaf weight, when treated with manganese sulfate via foliar spraying and priming at severe water deficiency (25% FC). In contrast, the Naz Takshakheh cultivar exhibited the lowest concentration of soluble sugar, at 0.374 mg $g^{-1}$ dry leaf weight, under well - watered conditions with manganese sulfate treatment (Fig. 4). Foliar application of 400 mg $L^{-1}$ manganese sulfate enhanced the levels of total carbohydrates, total protein, and antioxidant status in two cultivars of grapevine (*Vitis vinifera* cv. Rotabi, and Thompson seedless) subjected to water deficiency stress (Ghorbani *et al*., 2019). The increase in carbohydrate production in some plants treated with manganese sulfate may be linked to their higher chlorophyll content. Carbohydrate production is influenced by both the amount of chlorophyll and its efficiency (Lidon *et al*., 2004; Millaleo *et al*., 2010).

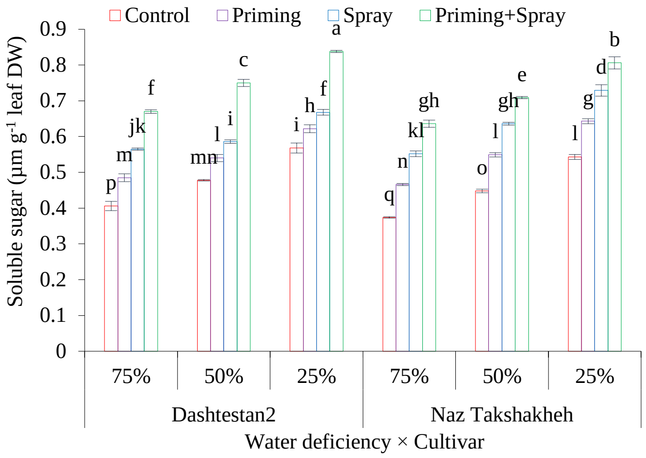

**Figure 4. The effect of different methods of manganese sulfate application on the soluble sugar content of two sesame cultivars under water-deficient stress conditions. Different letters indicate significant differences (p<0.05, Duncan's test).**

### *3.4. Soluble protein*

The mean comparison of data revealed a difference in soluble protein content between the two sesame cultivars. In the control treatment, the concentration of leaf soluble protein was 0.448 mg $g^{-1}$ FW for the Dashtestan2 cultivar, while it was 0.305 mg $g^{-1}$ FW for the Naz Takshakheh cultivar (Fig. 5). The experiment results indicated that seed priming with manganese sulfate enhanced the concentration of leaf soluble protein in both the Dashtestan2 and Naz Takshakheh cultivars. Specifically, the concentrations increased by 0.097 mg $g^{-1}$ of leaf FW for Dashtestan2 and 0.059 mg $g^{-1}$ for Naz Takshakheh, compared to the control treatment. These findings align with previous studies on wheat (Ahmad *et al*., 2019).

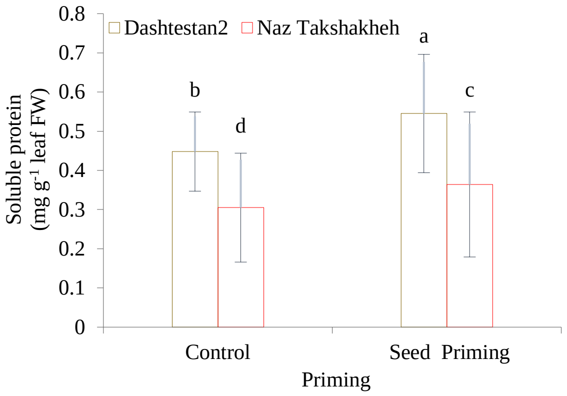

**Figure 5. The effect of seed priming on the soluble protein content of two sesame cultivars. Different letters indicate significant differences (p<0.05, Duncan's test).**

As water deficiency stress levels increased, the soluble protein content in both sesame cultivars decreased. In the Dashtestan2 and Naz Takshakheh cultivars, soluble protein levels dropped from 0.601 and 0.527 mg $g^{-1}$ leaf FW under well-watered conditions to 0.411 and 0.188 mg $g^{-1}$ leaf FW, respectively, under severe water deficiency (25% FC) conditions (Fig. 6). The results indicated that at varying levels of water deficiency stress, the soluble protein content of the Dashtestan2 cultivar was consistently higher than that of the Naz Takshakheh cultivar, with values of 0.074, 0.188, and 0.223 mg $g^{-1}$ of leaf FW, respectively (Fig. 6). Additionally, a study on wheat revealed that water deficiency stress conditions lead to a decrease in the protein content of wheat leaves (Ahmad *et al*., 2019).

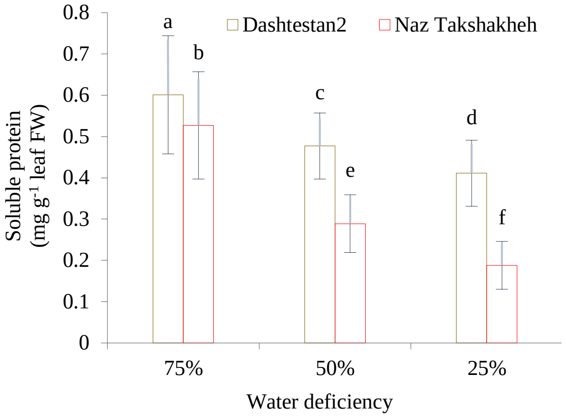

**Figure 6. The effect of water deficiency stress on the soluble protein content of two sesame cultivars. Different letters indicate significant differences (p<0.05, Duncan's test).**

The results demonstrate the beneficial effect of manganese sulfate foliar application on soluble protein levels under varying water deficiency conditions. As water deficiency stress intensified, the concentration of soluble protein in the leaves decreased. However, the application of manganese sulfate as a foliar treatment enhanced the soluble protein concentration at three levels of water deficiency stress, resulting in increases of 0.207, 0.126, and 0.116 mg $g^{-1}$ of leaf FW, respectively, compared to the control treatment (without foliar application) (Fig. 7). Fathi Amirkhiz et al. (2015) reported that the lack of manganese foliar application led to a decrease in protein content under water deficiency stress conditions. Manganese is effective in enhancing photosynthetic carbon conversion and drought tolerance by promoting the synthesis of soluble proteins and facilitating photosynthesis (Jafardokht *et al*., 2015). Foliar application of manganese sulfate can increase the protein content of grape leaves under water deficiency stress conditions (Lidon *et al*., 2004; Millaleo *et al*., 2010).

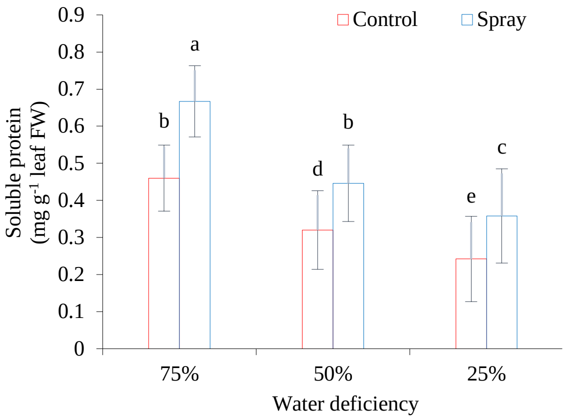

**Figure 7. The effect of foliar spraying of plants with manganese sulfate on the amount of leaf soluble protein under water deficiency stress conditions. Different letters indicate significant differences ($p<0.05$, Duncan's test).**

Seed priming reduced the negative impact of water deficiency stress on the concentration of soluble leaf protein. Specifically, under three levels of water deficiency stress, soluble sesame leaf protein increased by 0.137, 0.049, and 0.048 mg $g^{-1}$ of leaf FW, respectively, due to seed priming with manganese sulfate compared to the control treatment (without priming) (Fig. 8).

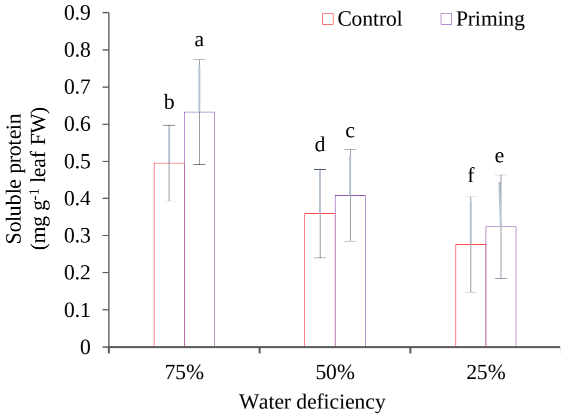

**Figure 8. The effect of seed priming with manganese sulfate on leaf soluble protein content under drought stress conditions. Different letters indicate significant differences ($p<0.05$, Duncan's test).**

### *3.5. CAT enzyme activity*

The results indicated that applying manganese sulfate through seed priming and foliar spraying enhanced CAT activity. Specifically, seed priming increased CAT activity by approximately 0.115 units, while foliar spraying resulted in a greater increase of about 0.148 units compared to the control treatment (Fig. 9). Manganese, an essential micronutrient, plays a crucial role in minimizing the production of oxygen-free radicals in plants caused by environmental stresses. It achieves this directly by enhancing the composition and activity of antioxidant enzymes, and indirectly by increasing the rates of photosynthesis and nitrogen metabolism (Waraich *et al.*, 2012).

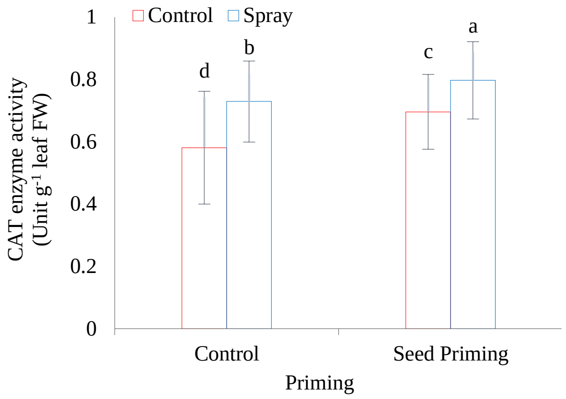

**Figure 9. The interaction effect of seed priming and manganese sulfate foliar application on CAT activity. Different letters indicate significant differences ($p<0.05$, Duncan's test).**

The results indicated that foliar application of manganese sulfate had a significantly greater impact on CAT activity than the seed priming method. Furthermore, CAT enzyme activity was higher in plants grown from primed seeds that also received foliar spraying with manganese sulfate, compared to those that underwent only seed priming or foliar spray treatment alone. As water deficiency stress levels increased, CAT enzyme activity also increased. The combined application of manganese sulfate through priming and foliar spraying further enhanced CAT activity under conditions of water deficiency stress. In the seed priming method, the activity of CAT enzyme increased by 0.208, 0.048, and 0.09 units compared to the control conditions (without seed priming and foliar spraying) at 75%, 50%, and 25% of field capacity, respectively (Fig. 10).

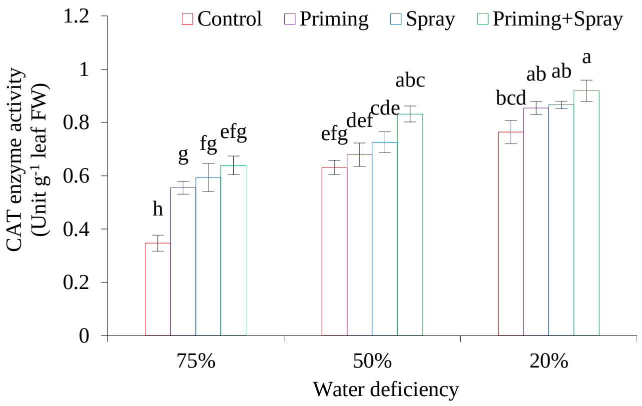

**Figure 10. The interaction effect of seed priming and manganese sulfate foliar application on CAT activity. Different letters indicate significant differences ($p<0.05$, Duncan's test).**

In the foliar spraying method, the increases were 0.247, 0.095, and 0.102 units, compared to the control conditions (without seed priming and foliar spraying). Additionally, the level of CAT enzyme activity increased more in the combined application method of seed priming and foliar spraying with manganese sulfate than in their separate application (Fig. 10). CAT is a heme-containing enzyme that catalyzes the conversion of hydrogen peroxide ($H_2O_2$) into water ($H_2O$) and oxygen ($O_2$) (Anjum *et al.*, 2016). During water deficiency stress conditions, the activity of CAT can vary; it may increase, decrease, or stay the same (Mishra and Panda, 2017). Increased activity of the CAT enzyme during water deficiency stress conditions helps eliminate $H_2O_2$, which in turn reduces cell damage and enhances the oxidative capacity of plants (Piri *et al.*, 2019). Antioxidant enzymes, such as CAT and SOD in safflower (Zafari *et al.*, 2020) and CAT and APX in castor (de Araújo Silva *et al.*, 2016), increased under water deficiency stress.

### 3.6. POX enzyme activity

The results indicated a difference in POX enzyme activity between the two sesame cultivars under all levels of water deficiency stress and manganese sulfate application methods. Specifically, the Dashtestan2 cultivar exhibited higher POX enzyme activity compared to the Naz Takshakheh cultivar. Various methods of applying manganese sulfate enhanced POX enzyme activity under all levels of water deficiency stress. Notably, the combined approach of seed priming and foliar spraying with manganese sulfate resulted in higher POX activity compared to each method applied separately. As water deficiency stress increased, POX enzyme activity rose in both sesame cultivars (Fig. 11). Similar findings have been reported in various plants, including maize (Shafiq *et al.*, 2021), faba bean (Siddiqui *et al.*, 2015), and mung bean (Abid *et al.*, 2017) under water deficiency stress conditions. Many researchers believe that the proper functioning of various enzymes, such as CAT, POX, and SOD, helps reduce the disruption of cellular stability caused by ROS (Hussain *et al.*, 2016; Ashraf, 2009; Moradi and Piri, 2018).

### 3.7. APX enzyme activity

Increasing water deficiency stress levels correlated with elevated activity of the APX enzyme in both sesame cultivars. However, there was a notable difference in enzyme activity between the two cultivars at all water deficiency stress levels. Specifically, in the Dashtestan2 cultivar, the APX activity at 75%, 50%, and 25% of FC was 0.081, 0.086, and 0.102 units higher than that of the Naz Takshakheh cultivar, respectively (Fig. 12). Studies on safflower (Khosrowshahi *et al.*, 2020) and milk thistle (ElSayed *et al.*, 2019) have indicated that water deficiency stress results in an increase in the activity of the APX enzyme. Similarly, research involving two canola cultivars—one sensitive and one tolerant-demonstrated that both cultivars exhibited increased APX enzyme activity under water deficiency stress conditions (Seyed Ebrahimi *et al.*, 2018).

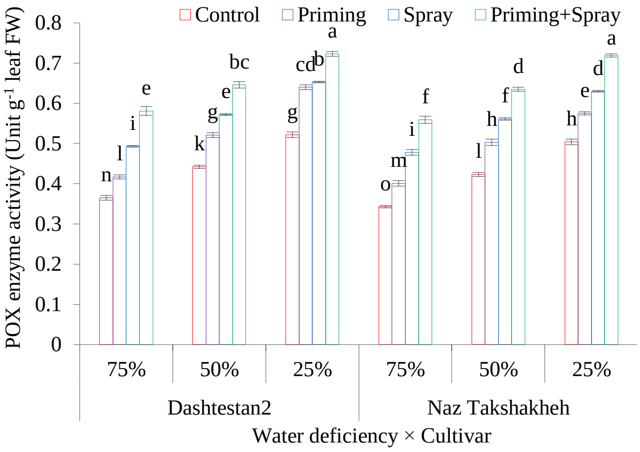

**Figure 11. The effect of different methods of manganese sulfate application on the POX activity of two sesame cultivars under water deficiency stress conditions. Different letters indicate significant differences (p<0.05, Duncan's test).**

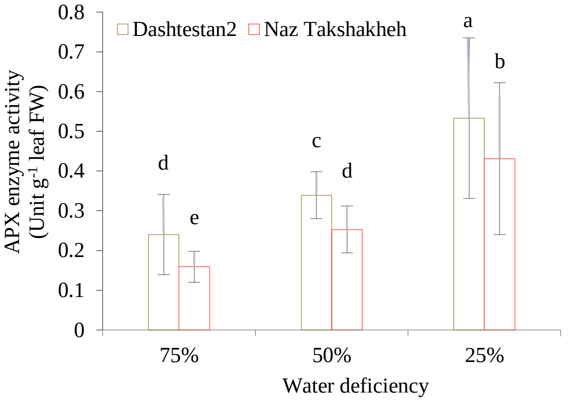

**Figure 12. The effect of water deficiency stress on the activity of APX enzyme in two sesame cultivars. Different letters indicate significant differences (p<0.05, Duncan's test).**

APX enzyme activity increased due to seed priming and the foliar application of manganese sulfate. Specifically, enzyme activity rose by 0.06, 0.138, and 0.258 units after seed priming, foliar spraying, and combined priming with solution spraying compared to the control treatment, respectively (Fig. 13). Similarly, a study by Jalili and Karimi (2022) on grapes found that foliar spraying with manganese also enhances POX enzyme activity.

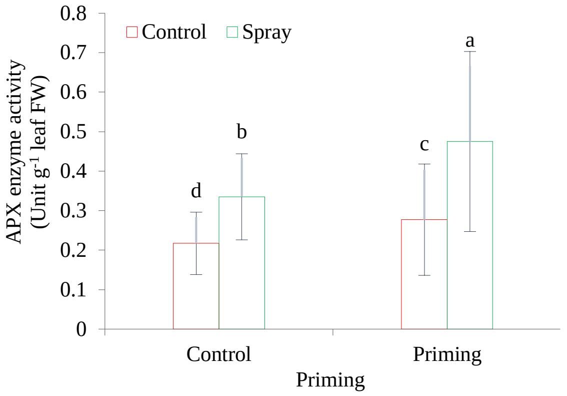

**Figure 13. The interaction effect of seed priming and foliar spraying with manganese sulfate on the activity of the APX enzyme. Different letters indicate significant differences (p<0.05, Duncan's test).**

As the level of water deficiency stress increased, the activity of APX increased from 0.151 units in the well watered condition (75% of FC) to 0.339 units in the severe water deficiency condition (25% FC). Foliar spraying of the plant with manganese sulfate led to an increase in the activity of APX at all levels of water deficiency stress compared to the control treatment. The activity of the APX enzyme increased by 0.097, 0.09, and 0.286 units compared to the control, with foliar spraying applied at 75, 50, and 25% of FC, respectively (Fig. 14).

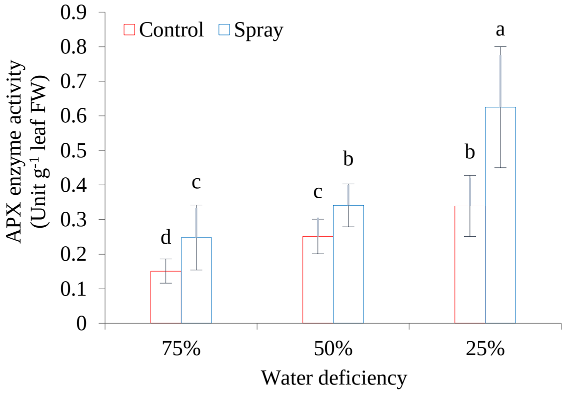

**Figure 14. The effect of manganese sulfate foliar application on APX enzyme activity under water deficiency stress conditions. Different letters indicate significant differences (p<0.05, Duncan's test).**

Compared to non-primed seeds, manganese sulfate priming boosted APX enzymatic function regardless of drought severity level. Specifically, seed priming at well watered (75% FC) increased enzyme activity by 0.077 units, at mild water deficiency (50% FC) by 0.044 units, and at severe water deficiency (25% FC) by 0.179 units compared to the control treatment (Fig. 15).

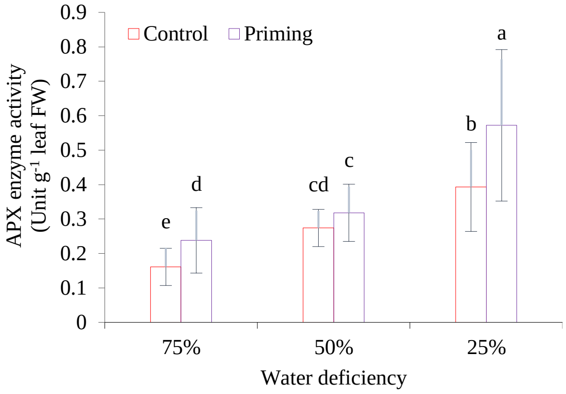

**Figure 15. The effect of seed priming with manganese sulfate on APX enzyme activity under water-deficient stress conditions. Different letters indicate significant differences (p<0.05, Duncan's test).**

## 4. Conclusion

This study found that water deficiency stress reduced both the seed yield and the soluble leaf protein content of the two sesame cultivars. Drought stress induced a dual response: osmotic adjustment via proline and sugar accumulation, coupled with enhanced antioxidant activity, such as CAT, POX, and APX activity. This study demonstrates that the combined seed priming and foliar application of $MnSO_4$ significantly outperformed either method applied individually, establishing a novel agronomic strategy for drought mitigation in sesame. Notably, cultivar-specific genetic variations in stress adaptation were identified, with Dashtestan2 exhibiting superior antioxidant defense activation and yield stability under water deficit conditions compared to Naz Takshakheh. Furthermore, the mechanistic linkage between $MnSO_4$-induced proline accumulation and enhanced antioxidant enzyme activity provides critical insights into micronutrient-mediated drought resilience, advancing our understanding of plant stress physiology. Future studies should explore the molecular basis of $MnSO_4$-induced drought tolerance in sesame, including transcriptomic analyses of stress-responsive pathways, while also optimizing field-level application protocols for diverse cultivars and environments. Additionally, investigating synergistic effects with other micronutrients or bio-stimulants could further enhance drought resilience strategies for sustainable sesame production under climate change.

## Conflict of interests

All authors declare no conflict of interest.

## Ethics approval and consent to participate

No humans or animals were used in the present research. The authors have adhered to ethical standards, including avoiding plagiarism, data fabrication, and double publication.

## Consent for publications

All authors read and approved the final manuscript for publication.

## Availability of data and material

All the data are embedded in the manuscript.

## Authors' contributions

All authors had an equal role in study design, work, statistical analysis and manuscript writing.

## Informed consent

The authors declare not to use any patients in this research.

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