Sulfate-Based Fertilizers Regulate Nutrient Uptake, Photosynthetic Gas Exchange, and Enzymatic Antioxidants to Increase Sunflower Growth and Yield Under Drought Stress

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Abstract

The challenging impact of drought to agricultural productivity requires the adoption of mitigation strategies with a better understanding of underlying mechanisms responsible for drought tolerance. The present study aimed at investigating the effects of sulfur-based fertilizers on mitigation of drought stress in sunflower. Sulfate-containing fertilizers, viz., ammonium sulfate, zinc sulfate, magnesium sulfate, potassium sulfate, and gypsum, were initially evaluated at two different rates (10 and 20 mg kg⁻¹ soil equivalent to 20 and 40 kg ha⁻¹, respectively) for nutrient uptake and growth-promoting traits in sunflower seedlings (cv. Hysun-33). The best performing fertilizer (gypsum) was then selected to evaluate the response of sunflower under drought stress imposed at flowering stage for three weeks (25–30% water holding capacity). Results indicated significant amelioration of drought stress with higher activity of photosynthetic apparatus, upregulation of antioxidative enzymes, and increased achene yield by gypsum application. In comparison to control, gypsum-treated plants (20 mg kg⁻¹ soil) exhibited higher water status (32%), leaf photosynthetic rate (29%), transpiration rate (67%), and stomatal conductance (118%) under drought stress. The antioxidant enzyme activities of catalase, guaiacol peroxidase, and superoxide dismutase were also increased by 67%, 62%, and 126%, respectively, resulting in higher achene yield (19%) under water-deficit conditions. This study indicates that the application of sulfur-based fertilizers (gypsum) can be used to induce drought tolerance and obtain high sunflower yields under drought stress, and furthermore, it is a cost-effective strategy resulting in high benefit–cost ratio with respect to no gypsum application.

Keywords Sulfur · Photosynthetic activity · Antioxidant machinery · Achene yield · Water stress · Sunflower

1 Introduction

Climate extremes such as drought have become the most common and critical limiting factors affecting the productivity of food crops around the globe (Leng and Hall 2019).

Low water availability not only impairs the germination and seedling establishment but also reduces the overall fitness of the plants to withstand unfavorable environmental conditions (Anavella et al. 2016). Drought-induced fluctuations at cellular level are related to the loss of turgor, reduced

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stomatal conductance, imbalance in membrane permeability, and accumulation of reactive oxygen species (ROS) (Shabbir et al. 2016; Hasan et al. 2021). Plants tend to adapt water limitations through various self-protection mechanisms, for instance, the regulation of stomatal aperture to adjust the photosynthetic capacity of mesophyll cells (Waseem et al. 2021). Also, the maintenance of optimal concentrations of mineral nutrients is highly important to support cellular metabolism under adverse conditions (Barzana et al. 2021). Therefore, knowledge about the management of nutrient fertilizers and cultivation of potential drought-tolerant crop species is crucial to combat the uncertainties associated with climate change (Ma et al. 2021).

Sunflower is considered a potential drought-tolerant oilseed crop in semi-arid regions (García-Vila and Fereres 2012) due to the presence of a complex branched root system that enables the plants to efficiently acquire water in dry soils (Keipp et al. 2020). However, severe arid or dry conditions drastically affect the early flowering and anthesis phase and may reduce the seed yield up to 80% (Pekcan et al. 2015; Hussain et al. 2016). The negative effects of drought stress on sunflower oil yield and quality are further aggravated by insufficient or imbalanced supply of mineral fertilizers (Khodaei-Joghan et al. 2018). Hence, the use of optimal fertilization practices is essential to achieve sustainable oilseed productivity in dry arid regions of the world (Yousaf et al. 2017).

Sulfur (S) is a key mineral nutrient that is involved in a wide variety of functions in plants (Kopriva et al. 2019). It is available to the plants as sulfate (SO_4^{2-}) and is the only macronutrient that accumulates in the xylem sap of plants exposed to water deficiency (Ernst et al. 2010). The application of SO_4^{2-} based inorganic fertilizers has gained special attention in the past few decades due to increased deficiency of S in agricultural soils. In plants, S deficiency decreases chlorophyll and Rubisco content and induces chlorosis in young leaves (Muneer et al. 2014; Chowdhury et al. 2020). On the contrary, the availability of S promotes the biosynthesis of proteins and chlorophyll (Fatma et al. 2014), regulates antioxidant enzymes (Usmani et al. 2020), and enhances the activity of photosynthetic apparatus under challenging environmental conditions including drought (Lee et al. 2016). Also, the requirement for S-containing metabolites for cellular metabolic reactions such as the biosynthesis of abscisic acid (ABA) and subsequent stomatal

closure implies the importance of S in plant growth under water limitations (Batool et al. 2018; Nawaz et al. 2019). Hasanuzzaman et al. (2018) suggested that the presence of SO_4^{2-} influences nutrient homeostasis and has a profound effect on the availability of essential nutrients in plants exposed to extreme environments. In addition, it also regulates the chemical composition of seed oil in oilseed crops (Ropelewska and Jankowski 2020).

While these studies provide valuable insights into S-mediated drought tolerance mechanisms in plants, very little is known about the effects of different sources of S on physiological mechanisms involved in improving growth and yield of oilseed crops under water-deficit conditions. This study partially fills the gap by investigating the effects of S-based fertilizers on growth and yield of sunflower. We hypothesized that the exogenous S supply induces several physiological and enzymatic alterations to confer drought tolerance in sunflower. Based on this hypothesis, the specific aims of the study were to (i) evaluate the effects of different S fertilizers on NPK uptake and biomass accumulation in sunflower and (ii) assess the beneficial effects of S-containing fertilizer on photosynthetic activity and antioxidant machinery to improve sunflower yield under water limitations.

2 Materials and Methods

To address the above-mentioned questions, we conducted two pot experiments in a naturally ventilated greenhouse under semi-controlled conditions. The experiments were carried out during the growth period of 2018 (February 05 to May 15), and the growth conditions in the greenhouse were as follows: ambient light (14–16 h sunshine), temperature (average 25–30 °C), and humidity (48%). The soil used in the experiments was collected from the B-block (experimental area) of MNS-University of Agriculture, Multan (longitude 71°29' E, latitude 30°10' N, altitude 122 m), Pakistan, and analyzed for various physicochemical characteristics (Table 1). Both experiments were conducted in a completely randomized design with three replicates. An indigenous sunflower hybrid, viz., Hysun-33 (ICI Pakistan Pvt. Ltd), reported as a drought-tolerant hybrid by Hussain et al. (2016), was used for the experiments.

Table 1 Physicochemical characteristics of soil used for the pot experiments

Physical properties		Chemical properties						
Texture	Water content (%)	EC (S/m)	pH	Organic Matter (%)	Available N (%)	Available P (mg kg ⁻¹)	Available K (mg kg ⁻¹)	Available S (%)
Sandy loam	9.2	2.47	8.1	0.79	0.082	4.50	160	0.035

2.1 Pot Experiment-I

The first experiment was done to evaluate the effects of various SO_4^{2-} fertilizers, viz., ammonium sulfate $[(\text{NH}_4)_2\text{SO}_4]$, zinc sulfate $[\text{ZnSO}_4]$, magnesium sulfate $[\text{MgSO}_4]$, potassium sulfate $[\text{K}_2\text{SO}_4]$, and gypsum $[\text{CaSO}_4 \cdot 2\text{H}_2\text{O}]$, and their two different levels (10 and 20 mg kg^{-1} soil equivalent to 20 and 40 kg ha^{-1}) on growth and shoot NPK concentrations of sunflower seedlings. The amount of fertilizer added to each pot was calculated following a general rule that the weight of a furrow slice of 1 hectare is approximately 2,000,000 or 2 million kg (Aboyeji 2019). By using this information, we calculated the amount of fertilizer to be applied to 12 kg soil, at a rate of 20 and 40 kg ha^{-1} , in each pot. The fertilizer doses for each SO_4^{2-} treatment and mineral nutrients (N, P, and K) were individually distributed and thoroughly mixed in the soil before filling the pots (diameter 30 cm, depth 48 cm). The experiment consisted of 33 pots, i.e., 11 treatments replicated three times, no application of SO_4^{2-} fertilizer as control, and application of two levels (20 and 40 kg ha^{-1}) of five different S-containing fertilizers, viz., $(\text{NH}_4)_2\text{SO}_4$, ZnSO_4 , MgSO_4 , K_2SO_4 , and $\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$. Initially, five seeds were sown in each pot, which were later thinned after germination to maintain three healthy sunflower seedlings till harvest. The plant nutrient requirements for base fertilizers (NPK) were met using urea, diammonium phosphate, and potassium hydroxide as described in our previous study (for details, please see Shehzad et al. 2020). However, the additional amount of N and K supplied by $(\text{NH}_4)_2\text{SO}_4$ and K_2SO_4 , respectively, was removed from the total nutritional requirements for NPK fertilizers. The randomly selected, physically pure seeds (five seeds per pot) of Hysun-33 were sown at 2 cm depth in pots.

The procedure reported by Öhlinger (1996) was followed to determine the water holding capacity (WHC) of soil, which was adjusted to 65–70% for well-watered plants. The water loss was estimated gravimetrically, and the plants were watered daily with de-ionized water to maintain the soil moisture levels at 65–70% WHC. The plants were grown for 4 weeks and were harvested after 32 days (DAS) to estimate the biomass and shoot nutrient concentrations.

2.2 Pot Experiment-II

Based on the results obtained from pot experiment-I, a second pot experiment was performed using the best performing SO_4^{2-} fertilizer (gypsum) to understand the physiological and biochemical basis of drought tolerance in sunflower. The soil was separately mixed with four different gypsum levels, i.e., 0, 10, 15, and 20 mg kg^{-1} soil (equivalent to 20, 30, and 40 kg S ha^{-1}), and later filled in the pots (diameter 30 cm, depth 48 cm) prior to sowing. The experiment consisted of

24 pots, which were divided into two main groups, i.e., normal and drought that consisted of four subgroups for gypsum treatments (0, 20, 30, and 40 kg ha^{-1}). Every treatment consisted of three replicates, and three healthy sunflower plants were grown till maturity in each replicate. All other operations such as the soil volume in each pot, growth conditions, and mineral fertilizer (NPK) requirements were the same as described earlier.

All plants were grown for 6 weeks under well-watered conditions (65–70% WHC). Afterwards, the soil moisture level was gradually reduced to 25–30% WHC (drought stress phase) in one set of the pots and maintained for further 3 weeks (flowering stage). The pots were weighed daily to record soil moisture content and later supplemented with water to compensate the evapotranspiration losses. The leaf samples were collected for the measurement of relative water content (RWC) and enzymatic activity of antioxidants at this stage. Moreover, leaf chlorophyll content (estimated as soil plant analysis development or SPAD value) and gas exchange characteristics were also recorded. At the end of the drought stress phase, the soil moisture content of water-stressed plants was raised and kept to the normal 65–70% WHC till physiological maturity. The harvested plant material was later used to estimate the yield and yield attributes.

2.3 Determination of Growth Attributes and Nutrient Content

Two fresh seedlings were randomly selected from each pot, immediately weighed for fresh weight (SFW), and afterwards kept in a plastic bag to determine the dry weight (SDW), shoot length (SL), and root length (RL). The SL and RL were determined using a meter scale, whereas the seedlings were dried at 65 °C for 48 h to estimate SDW.

The effects of S fertilization on shoot N, P, and K concentrations of sunflower were estimated using standard procedures (Wolf 1982). The accumulation of N was determined using Kjeldhal method, whereas the vanadium molybdate yellow colorimetric method and flame photometer (Sherwood M410, UK) were used to estimate the P and K concentrations.

2.4 Determination of Leaf SPAD Value and RWC

Leaf SPAD value was determined using SPAD-502 (Minolta, Japan). The observations were recorded from the randomly selected, fully expanded uppermost leaves between 9.00 and 11.00 am early in the morning. The average of five SPAD

values was considered as the leaf Chl content for each treatment.

To measure the leaf RWC, young and fully expanded top most leaves were collected, weighed immediately to estimate fresh weight (FW), and later dipped in the ice cold distilled water (4 °C) for 24 h. Afterwards, the leaves were taken out to record the turgor weight (TW) and later oven-dried at 65 °C for 72 h to estimate the dry weight (DW) as reported by Matin et al. (1989):

$$\text{RWC} = \left[(\text{FW} - \text{DW}) / (\text{TW} - \text{DW}) \right] \times 100$$

2.5 Gas Exchange Characteristics

The leaf gas exchange characteristics such as net photosynthetic rate (A), transpiration rate (E), and stomatal conductance (g_s) were measured from the upper fully expanded leaf with a portable open-flow CIRAS-3 gas exchange meter (PP systems, Amesbury, USA). The observations were recorded in early hours of morning (9:00 to 11:00 am) using the instrumental settings as described in Shehzad et al. (2020).

2.6 Determination of Antioxidant Enzymes Activity

Frozen leaf samples (0.5 g) were thawed and later homologized using mortar and pestle in a medium containing 5 ml extraction buffer (50 mM Na_2HPO_4 pH 7.0 and 1 mM dithiothreitol). The sample mixture was then centrifuged ($20,000 \times g$ 15 min) at 4 °C and then used to assay superoxide dismutase (SOD), guaiacol peroxidase (GPX), and catalase (CAT) activity.

The enzymatic activity of SOD was estimated following the method of Van Rossum et al. (1997), whereas the GPX activity was recorded according to the method of Urbanek et al. (1991). To determine the CAT activity, we followed the procedure reported by Aebi (1984).

2.7 Yield Attributes

Three sunflower plants for each treatment were manually harvested at physiologically maturity. The achenes were then separated from achene head, counted to determine the number of achenes per head (AH) and then weighed to calculate the 1000-achene weight (GW). Later, the biological yield (BY) and achene yield (GY) were estimated and recalculated to tons per hectare (t ha^{-1}).

2.8 Economic Analysis

The analysis of benefit–cost ratio was carried out to evaluate the economic feasibility of different S doses to alleviate the drastic influence of water deficiency in sunflower. The gross

income was estimated by using prevailing average marketing price in Pakistan, PKR 4400 per 40 kg.

2.9 Statistical Analysis

The statistical analyses were performed using STATISTIX 8.1. The probability level was maintained at 5% to compare treatment means with post hoc Tukey test using ANOVA (analysis of variance) technique.

3 Results

3.1 Growth Attributes and NPK Content

Treatment of sunflower seedlings with various S sources considerably ($P \leq 0.001$) increased shoot length (SL), root length (RL), plant fresh weight (SFW), and plant dry weight (SDW) (Supplementary Table 1). The highest increase in SL (115%), SFW (95%), and SDW (135%) was noted in seedlings treated with gypsum ($\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$) at 40 kg ha^{-1} compared to control, i.e., no S supply (0 kg ha^{-1}). A marked increase in these growth attributes was also noted by $(\text{NH}_4)_2\text{SO}_4$ application at 40 kg ha^{-1} that increased SL, RL, SFW, and SDW by 76, 70, 54, and 40%, respectively, compared to control (Fig. 1a–d).

Sunflower seedlings applied with various S sources exhibited marked ($P \leq 0.001$) variation for shoot N, P, and K concentrations (Supplementary Table 1). The highest increase in N (35%) and P (39%) concentrations was observed in seedlings treated with $\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$ at 40 kg ha^{-1} (Fig. 2a, c), whereas the seedlings treated with K_2SO_4 at 40 kg ha^{-1} exhibited the highest increase in K content (20%) statistically at par with $\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$ (19%) and $(\text{NH}_4)_2\text{SO}_4$ (18%) with respect to control (Fig. 2c). The application of high dose of K_2SO_4 also significantly increased the shoot N (26%) and P (22%) content compared to control. Interestingly, the sunflower seedlings treated with MgSO_4 (20 kg ha^{-1}) gave the lowest values in terms of shoot N, P, and K content (Fig. 2a–c).

3.2 Leaf Chlorophyll and Relative Water Content

Drought stress considerably ($P \leq 0.001$) decreased the leaf Chl of sunflower (Supplementary Table 2) and induced a reduction of 22% compared to normal ones. The gypsum supply significantly ($P \leq 0.001$) ameliorated the negative effects of droughts stress with maximum value (40.43 SPAD value) recorded in the leaves of plants supplemented with 40 kg ha^{-1} gypsum. A significant increase of 25% was also noted in the plants fertilized with gypsum at

Fig. 1 Effect of various sulfur sources and levels on shoot length (a), root length (b), fresh weight (c), and dry weight (d) of sunflower seedlings under well-watered conditions. The mean values with different letters indicate significant difference ($P \leq 0.05$), according to post hoc Tukey's test

30 kg ha⁻¹ compared to no gypsum application (Fig. 3a). Similar to leaf Chl, the exposure to drought stress markedly ($P \leq 0.001$) reduced (50%) the leaf RWC of sunflower (Supplementary Table 2). Gypsum application considerably influenced ($P \leq 0.001$) the leaf RWC and improved it by 32% (40 kg ha⁻¹) and 26% (30 kg ha⁻¹) with respect to control, i.e., no gypsum supply under water-deficit conditions (Fig. 3b).

3.3 Leaf Gas Exchange Characteristics

Two-way ANOVA showed the significant interactive effects of drought stress (D) and gypsum doses (G) on the leaf A , E , and g_s of sunflower plants (Supplementary Table 2). There was a significant effect of drought stress on A (20%), E (43%), and g_s (86%) of sunflower. Compared to no gypsum application (control), treatment with 40 kg ha⁻¹ gypsum enhanced A , E , and g_s by 29%, 67%, and 118%, respectively, under water-deficient conditions (Fig. 4a–d). The gypsum application at 30 kg ha⁻¹ also had a significant effect on A (10%) and E (40) (Fig. 4a, b), whereas it did not significantly influence the g_s in water-stressed plants (Fig. 4c, d).

ferent letters indicate significant difference ($P \leq 0.05$), according to post hoc Tukey's test

3.4 Antioxidant Enzyme Activity

The enzymatic activity of catalase (CAT), guaiacol peroxidase (GPX), and superoxide dismutase (SOD) were significantly ($P \leq 0.001$) influenced by drought stress (Supplementary Table 3). The water-stressed sunflower plants exhibited 25, 63, and 42% higher CAT, GPX, and SOD activities, respectively, compared to normal ones. A significant variation ($P \leq 0.001$) was also noted among various gypsum doses as the highest increment in CAT (67%), GPX (62%), and SOD (126%) was observed in the plants supplemented with 40 kg ha⁻¹ gypsum under drought stress (Fig. 5a–c). Likewise, the gypsum fertilization at 30 kg ha⁻¹ also enhanced ($P \leq 0.001$) the antioxidant activity of CAT, GPX, and SOD by 27%, 26%, and 69% in water-stressed sunflower plants, whereas the low gypsum dose of 10 kg ha⁻¹ did not significantly influence the antioxidant enzymes compared to control (no gypsum application).

3.5 Yield Attributes

As shown in two-way ANOVA (Supplementary Table 3), the yield attributes of sunflower were significantly affected by drought stress resulting in a decrease of 17%, 29%, 19%, and 6% in achene per head (AH), 1000-achene weight (GW), achene yield (GY), and biological yield (GY) (Supplementary Table 3). The gypsum application had

Fig. 2 Effect of various sulfur sources and levels on shoot nitrogen (a), phosphorous (b), and potassium content (c) of sunflower seedlings under well-watered conditions. The mean values with different letters indicate significant difference ($P \leq 0.05$), according to post hoc Tukey's test

significant effects on yield attributes, except for low gypsum dose of 10 kg ha⁻¹. By increasing gypsum dose, the yield attributes were considerably increased in sunflower plants. The plants supplemented with gypsum at 40 kg ha⁻¹ exhibited 19, 36, 33, and 7% higher AH, GW, GY, and BY, respectively, than no gypsum supply under drought stress conditions (Fig. 6a-d).

The economic analysis revealed that optimum gypsum application helped to reduce drought-induced damages to

crop yield and improved the net on farm income. Under drought conditions, the highest benefit to cost ratio (1.14) was noted in plants grown in the soil supplemented with 40 kg ha⁻¹ gypsum (Table 2).

Fig. 3 Effect of different gypsum levels on leaf chlorophyll (a) and relative water content (b) of sunflower under well-watered and drought stress conditions. The mean values with different letters indicate significant difference ($P \leq 0.05$), according to post hoc Tukey's test

4 Discussion

Deficiency of S in oilseeds is expected to intensify in coming years due to decreased supply of S fertilizers, cultivation of large number of crops in one season, and illogical use of plants for feed and fuel purpose. Moreover, erosion and leaching have further degraded the soil contributing to S deficiency in soils (Nawaz et al. 2019). During the past few decades, the protective role of S-containing compounds against abiotic stresses has been investigated in detail (Hasanuzzaman et al. 2018). Exposure to water stress regulates S partitioning in 229 different ways compared to nitrate and phosphate (Ernst et al. 2010). Drought stress upregulates the uptake of SO_4^{2-} compared to other ions, reflecting a higher demand of S in source organs under water-deficit conditions. Consequently, the influx of SO_4^{2-} from xylem stimulates ABA synthesis to initiate stomatal closure in the leaves during early stages of water stress (Shekoofa and Sinclair 2020).

Total S requirement varies among crop species and also depends upon the development stages of the plant. In general, oilseeds require more S than cereal crops, owing to the

Fig. 4 Effect of different gypsum levels on leaf photosynthetic rate (a), transpiration rate (b), and stomatal conductance (c) of sunflower under well-watered and drought stress conditions. The mean values with different letters indicate significant difference ($P \leq 0.05$), according to post hoc Tukey's test

high S demand for oil biosynthesis (Al Murad et al. 2020). S is an essential element required for the formation of chlorophyll and promotes photosynthetic activity to increase growth and biomass accumulation in plants (Muneer et al. 2014). Drought stress negatively influences photosynthesis and restricts the transformation of photosynthates in plant biomass (Nawaz et al. 2015; Vicente-Serrano et al. 2020). In the present study, drought-induced reduction in biomass might be associated to impaired cell division, decreased photosynthetic rate, restriction in nutrient acquisition, or a

Fig. 5 Effect of different gypsum levels on enzymatic activity of catalase (a), guaiacol peroxidase (b), and superoxide dismutase activity (c) of sunflower under well-watered and drought stress conditions. The mean values with different letters indicate significant difference ($P \leq 0.05$), according to post hoc Tukey's test

combination of all these factors (Khan et al. 2017). Water stress induces protoplasm dehydration (Abdelaal et al. 2020) and decreases cell elongation and expansion due to the loss of turgor (Sun et al. 2020). Our results showed that gypsum supply resulted in higher SL and plant biomass than other SO_4^{2-} -based fertilizers (Fig. 1a–d). Mariño Macana et al. (2020) suggested that the positive effects of

gypsum application on plant growth are associated to the increase in fine root distribution and higher availability of certain nutrients such as calcium (Ca), magnesium (Mg), and SO_4^{2-} in the soil profile. Moreover, gypsum stabilizes soil structure by increasing flocculation in the soil, enhances cation exchange capacity, and improves soil infiltration rate (Chibowski et al. 2014). Müller et al. (2012) showed that soil amendment with gypsum promotes the vertical mobility and hydraulic gradient of the soil profile, consequently increasing water and nutrient uptake in plants.

A marked increment in shoot NPK content was observed by the application of SO_4^{2-} -based fertilizers in sunflower (Fig. 2a–c), providing further evidence that S supply considerably increases nutrient content to promote vegetative growth in sunflower (Matraszek et al. 2015). High shoot N concentration by S application indicates the synergistic interactions between both elements, also reported by Lee et al. (2016) in *Brassica napus*. Etienne et al. (2018) showed that the remobilization of SO_4^{2-} in vacuole triggers NO_3^- and PO_4^{3-} accumulation that might help to maintain the osmotic potential in leaves. In comparison to other SO_4^{2-} sources, gypsum application at 40 kg ha⁻¹ resulted in higher NPK concentrations in sunflower (Fig. 2a). This increase might be associated to the ability of gypsum to promote the formation of fine roots in subsoil, thereby increasing water and nutrient uptake in plants (Mariño Macana et al. 2020). Also, gypsum supply stimulates PO_4^{3-} adsorption and decreases the solubility of organic P by increasing flocculation and ionic strength of soil particles (Batte and Forster 2015). Consistent with our findings, Smagula and McGovern (2012) reported a significant increase in leaf N and P concentrations of *Vaccinium angustifolium* Ait plants treated with combined gypsum and DAP. In the present study, a significant increase in shoot K concentration was also observed in plants supplemented with gypsum at 40 kg ha⁻¹, closely followed by $(\text{NH}_4)_2\text{SO}_4$ and K_2SO_4 application (Fig. 2c). Shekhi Shahrivar and Khademi (2018) suggested that the addition of gypsum increases Ca concentration and changes the equilibrium of K in the root zone and plant tissues. Similarly, the increased availability of K and its importance in N metabolism could be the reason for high K concentration in plants treated with $(\text{NH}_4)_2\text{SO}_4$ and K_2SO_4 (Barlóg et al. 2019).

Drought stress significantly reduced the leaf water status and gave the lowest leaf RWC in control (no gypsum application) plants (Fig. 3a). The decline in leaf RWC under water limitations is associated to low tissue water potential (Nawaz et al. 2012). It was observed that gypsum application considerably alleviated the negative effects of drought stress by increasing the leaf RWC (Fig. 3b). This indicates the potential of gypsum to alter the soil water holding capacity to promote water movements in dry soils (Chi et al. 2012). Soil amendments with mineral elements like gypsum enhance soil aggregation and porosity and improve the water

Fig. 6 Effect of different gypsum levels on number of achenes per head (a), 1000-grain weight (b), achene yield (c), and biological yield (d) of sunflower under well-watered and drought stress conditions.

The mean values with different letters indicate significant difference ($P \leq 0.05$), according to post hoc Tukey's test

retention capacity of soil (Batoool et al. 2015). Moreover, gypsum can hold water molecules in its crystalline structure, which could be the potential source of moisture for plants under dry conditions (Palacio et al. 2014). A considerable decrease in the SPAD value (Chl content) was recorded in the leaves of sunflower plants with no gypsum treatment under drought stress (Fig. 3a). The reduction in Chl content is an indicator of drought-induced damage to the chloroplast, which is further aggravated by S-deprivation, causing

chlorosis in young leaves (Muneer et al. 2014). It is well-established that S-derived metabolites are important constituent of amino acids, methionine, and proteins required for chlorophyll biosynthesis (Abadie and Tcherkez 2019). The beneficial effects of gypsum application on chloroplast health were evident by the increased SPAD value, which helped to maintain chlorophyll, and inhibited the destruction of photosynthetic pigments under extreme conditions (Al-Huqail et al. 2017). These findings suggest that the use of

Table 2 Effect of gypsum application on net income and benefit cost ratio of sunflower under normal and drought conditions

Gypsum treatments	Total expenditure (*US \$ ha ⁻¹)		Gross income (*US \$ ha ⁻¹)		Net income (*US \$ ha ⁻¹)		Benefit to cost ratio	
	Well-watered	Drought	Well-watered	Drought	Well-watered	Drought	Well-watered	Drought
0 kg ha ⁻¹ (control)	534.18	524.18	562.5	481.3	90.83	-19.58	1.15	0.91
20 kg ha ⁻¹	537.43	527.43	660	515.63	122.58	-44.45	1.23	0.98
30 kg ha ⁻¹	539.05	529.1	756.25	563.76	217.2	34.7	1.4	1.07
40 kg ha ⁻¹	540.68	530.68	776.88	605	236.2	199.325	1.44	1.14

* 1.00 US \$ $\cong$ 160 PKR

appropriate S fertilizer like gypsum can alleviate the negative effects of S deficiency on functional chloroplasts, which are generally rich in S and play a key role in photosynthesis (Chowdhury et al. 2020).

Drought-mediated stomatal closure significantly reduced the photosynthetic rate (A), transpiration (E), and stomatal conductance (g_s) of sunflower plants (Fig. 4). The reduction in leaf gas exchange characteristics is considered the first line of defense against drought stress (Hasan et al. 2021). The application of gypsum helped in the restoration of photosynthetic efficiency by regulating the activity of stomatal aperture (Fig. 4c), resulting in enhanced A and E . These positive effects of gypsum supply might be due to the increased availability of S for the formation of S-containing compounds that interact with ABA to increase K^+ influx into guard cells, consequently improving photosynthetic activity under drought stress (Han et al. 2019). Moreover, it may be inferred that gypsum application enhanced the hydraulic gradient of soil profile to permit an increased water supply for improved photosynthesis under water-deficit conditions. In this study, the application of gypsum at 40 kg ha^{-1} gave the highest increase in A , E , and g_s as compared to low doses (20 and 30 kg ha^{-1}) or no gypsum supply (control). Similar to our results, Hu et al. (2014) demonstrated that S availability influences stomatal closure in epidermal strips of sweet potato in a dose-dependent manner. Also, the excess S supply increases the protein and chlorophyll biosynthesis and stimulates Rubisco to improve photosynthesis under adverse conditions (Fatma et al. 2014). However, the use of very high S doses may also cause toxicity by enhancing the production of ROS leading to non-apoptotic death of guard cells (Ooi et al. 2019).

Drought stress induces the overproduction of ROS-including highly toxic O_2^- and H_2O_2 that damage cell machinery through redox imbalance and oxidative stress (Shabbir et al. 2016). The ability to maintain higher antioxidant activity under stress conditions is essential to prevent potential damages of H_2O_2 to biomolecules and cell membrane (Hu et al. 2015). S is a vital element that regulates the synthesis of vital proteins and regulates the enzymatic activities of antioxidants to reduce oxidative damage (Sarker and Oba 2018). Accordingly, gypsum supplemented plants exhibited reduced effects of drought stress that could be associated to the upregulation of catalase (CAT), guaiacol peroxidase (GPX), and superoxide dismutase (SOD) (Fig. 5a–c). The enhanced activity of antioxidant machinery by gypsum application may be due to S availability that activates the primary ROS scavengers like glutathione to reduce lipid peroxidation under water limitations (Kopriva et al. 2019). Moreover, gypsum application increases Ca content in plants that also plays a regulatory role in plant cell metabolism to stabilize lipid bilayer and decreases ROS-induced H_2O_2 production under extreme conditions (Ahmad et al.

2015). Such results suggest that gypsum-mediated stimulation of antioxidant enzymes ensured the maintenance of leaf water status (Fig. 3a) and gas exchange attributes (Fig. 4) capable of sustaining sunflower growth under drought stress. Smaoui-Jardak et al. (2017) also reported the increase in antioxidant activity by phosphogypsum application to confer salinity and metal stress tolerance in tomato.

The positive effects of gypsum on crop yields are well reported (Wolkowski et al. 2010; Chen and Dic 2011; Ekholm et al. 2012). Gypsum improves soil physical properties and promotes flocculation by reducing soil dispersion (Batte and Forster 2015). Rhoton and McChesney (2011) reported significant increase in water infiltration and moisture content of soils fertilized with gypsum. They suggested that gypsum supply considerably reduces runoff and serves as a readily available source of SO_4^{2-} and Ca^{2+} to improve crop yield. In the present study, gypsum-mediated increase in sunflower yield may also be associated to improved leaf water status and regulation of photosynthetic apparatus under water-deficit conditions. The beneficial effects of gypsum on achenes per head (AH) and 1000 grain weight (GW) suggests that it regulates water transport, partially due to improved deep rooting and increased nutrient uptake, to maintain assimilate partitioning and sink capacity under water-limited conditions (Ekholm et al. 2012). Moreover, the presence of SO_4^{2-} in gypsum regulates S assimilation pathway enzymes including antioxidants such as CAT, GPX, and SOD to reduce ROS-induced damages, consequently improving yield under water-deficit conditions (Usmani et al. 2020).

5 Conclusion

In conclusion, our results showed that the response of sunflower seedlings varies with respect to the type of sulfate fertilizer. Gypsum application gave the highest increase in biomass and concentration of mineral nutrients as compared to other sulfate-based fertilizers. Also, the addition of gypsum at 40 kg ha^{-1} considerably alleviated the negative effects of drought stress by increasing the leaf water status, photosynthetic efficiency, and activity of antioxidant enzymes, all of which contributed to enhance sunflower yield under water-deficit conditions. Moreover, the use of gypsum was found cost-effective, which is likely to be advantageous to agronomic and economic aspects of sunflower cultivation in dry soils. Given the importance of gypsum as one of the cheapest sources of sulfur, our results have important implications for increasing sunflower yield under arid conditions.

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Declarations

Competing interest The authors declare no competing interests.

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