Research Article

Seed Priming with Thiourea Enhances the Performance of Sesame (*Sesamum indicum* L.) Varieties Under Salinity Stress

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Abstract | Salinity is most significant abiotic factor limiting sesame growth, physio-chemical mechanisms and productivity. To address this issue a pot trial was conducted to check the effectiveness of hydropriming (water; control), thiourea (150 mM) seed priming under normal (10.8 mM) and saline conditions (70 mM). The seeds of two varieties (TS-05 and TH-06) was sown at Botany Garden, University of Agriculture, Faisalabad. Results showed that salinity decreases the growth (root and shoot parameters) impaired the balance between antioxidants (superoxide dismutase, catalase, peroxidase) and oxidants (hydrogen peroxide and malondialdehyde), and lessened the uptake of essential minerals (potassium and calcium) irrespective of varietal differences. However, the performance of TH-6 was better than TS-5. In addition, the seed priming of thiourea enhanced the sesame photosynthetic pigments and efficiency, secondary metabolites production, antioxidant machinery, and nutrient uptake in both varieties which increased growth and development as a result. So, thiourea seed priming is an effective strategy to counteract the negative effects of salt stress by improving tolerance mechanisms.

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Introduction

Sesame (*Sesamum indicum* L.) belonging to the Pedaliaceae family possesses the title queen of oilseeds owing to its superior oil quality along with beneficial compounds like sterols, sesamin, sesamolin, and tocopherols, which serve as nutraceuticals contributing to various physiological and nutritional advantages (Langyan *et al*., 2022). The growth of sesame plants is sustained by tropical, subtropical, and southern temperate regions. Leading sesame-exporting countries include China, Myanmar, India, and Sudan (Chen *et al*., 2020). Sesame can replace animal proteins and fats used in human food

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because it contains a plenty of fats and plant proteins (Rahman *et al*., 2020) and seeds of sesame are rich in oil contents ranging from 45% to 63% (Biswas *et al*., 2018). Additionally, it is a valuable source of minerals, fibers, and vitamins (Zebib *et al*., 2015). Furthermore, sesame possesses antioxidant properties which render it a desirable ingredient in pharmaceutical formulations (Wan *et al*., 2023).

Besides its significance, various climatic factors impact the productivity of sesame. Sesame cultivation is challenged by the occurrence of multiple abiotic stresses consequently leading to a reduction in yield (Wang *et al*., 2021). Several abiotic stresses such as drought, waterlogging, salt, and heat have an impact on sesame efficiency, yield, and seed quality (Dossa *et al*., 2019). The most significant abiotic factor limiting sesame growth and productivity is salinity. Salt stress influences emergence, growth and yield potential (Kanagaraj and Sathish, 2017). Salt stress has three major effects on plant growth including reduced soil water potential known as osmotic stress, ionic imbalance in cells and ion toxicity (Franzisky *et al*., 2023; Hualpa-Ramirez *et al*., 2024). Salinity affects a variety of physiological processes including transpiration, stomatal conductance, photosynthesis, water potential and ultimately declines the growth and yield production (Desingh and Kanagaraj, 2019; Taratima *et al*., 2023; Victoria *et al*., 2023). During salt stress conditions, the substantial amount of salt in the leaf reduces water potential. The presence of an elevated level of salts in the leaf caused the stomata to close which reduced transpiration and CO_2 resulting in decreased photosynthesis (Rangani *et al*., 2016). Salt stress inhibits photosynthesis by triggering closure of stomata and averting the diffusion of CO_2 (Zahra *et al*., 2022a). Saline stress may also influence non-stomatal properties like chlorophyll synthesis, photosystem structure, and electron transport (Pan *et al*., 2021).

To mitigate the negative effects of salinity in sesame various strategies were used including seed priming (Tariq and Shahbaz, 2020), plant growth-promoting rhizobacteria (Khademian *et al*., 2019), and effective use of nitrogen fertilizers (Waqas *et al*., 2023) and other fertilizers application (Mahdavi-Khorami *et al*., 2020; Dollison and Dollison, 2023). Thiourea (TU) which is a sulfur and nitrogen-containing compound, is an important plant growth regulator that influences plant growth, particularly under stressed conditions (Hafeez *et al*., 2024). Thiourea can reduce oxidative stress-induced growth impairment by increasing the activity of antioxidant enzymes involved in ROS scavenging and modulating calcium signaling, redox state, and hormonal homeostasis (Ahmad *et al*., 2022a). Farooq *et al*. (2023), reported that the application of foliar thiourea increased the activity of peroxidase (POD) and potassium (K) levels in roots under salt stress conditions. Additionally, it led to elevated levels of chlorophyll b, total chlorophyll, and carotenoids. Overall, it can be concluded that foliar application of thiourea mitigated the negative effects of salinity by enhancing potassium ion content and antioxidant activity including peroxidase. Similarly, in another study Jhanji and Dhingra (2020) the germination characteristics of unsoaked seeds, hydroprimed seeds, and thiourea-primed seeds (at 750 ppm concentration) were examined under varying conditions of water and NaCl (30 and 50 mM). However, foliar application of thiourea on sesame have been reported by Dhillon *et al*. (2023) under salinity, and Sonia *et al*. (2024) under drought. However, there is no study present on seed priming with thiourea to mitigate the adverse effects of salinity in sesame. Hypothetically, thiourea seed priming may enhance growth, physio-chemical processes under salinity stress. Therefore, the present study was proposed to assess the impact of thiourea seed priming to mitigate the salt stress effect in sesame.

Materials and Methods

Experimental detail

The pot experiment was conducted at Botany Garden, University of Agriculture, Faisalabad and the experimental design was used complete randomized design (CRD) with 3 way factorial arrangements to check the effectiveness of thiourea (150 mM) seed priming under normal (10.8 mM) and saline conditions (70 mM). The seeds of these two varieties (TS-05 and TH-06) obtained from Oil Seed Research Institute, Faisalabad) were soaked in the 150 mM solution of thiourea for 16 hours. Then, seeds of varieties were sown in soil (autoclave at 121°C for 120 minutes) with ten seeds in each pot. The size of each pot having the dimensions 14 inch width and 16 inch depth were filled with 10 kg of soil. After seed germination five plants per pot were maintained. Salinity stress was imposed after one week of germination in each pot, the salt stress (0 and 70 mM) was imposed after germination of seeds in increments of 35 mM initially and then was attained to the 70 mM and sodium chloride (NaCl) was used for salinity imposition and the harvesting was done after one month of sowing date for growth and biochemical analysis. The growth parameters including root length, shoot length, root and shoot fresh weight were determined.

Nutrient content

Root and shoot samples were digested following the procedure described by Wolf (1982). Initially, 0.1 g of dry root and shoot sample was placed in a digestion flask containing 2 mL of concentrated hydrogen sulfate and allowed to stand overnight. The subsequent day, the sample underwent heating on a hot plate at 50°C for an hour. After removing the hydrogen peroxide (2 mL) was mixed in the sample, followed by continued heating until the sample became colorless. To make a volume of 50 mL, distilled water was added. The resulting solution was then filtered, and the filtered sample was utilized to determine the concentrations of K^+, Na^+, and Ca^{2+} using a flame photometer.

Photosynthetic pigments

The method of Arnon (1949) and Takaichi *et al.* (1995) was used to measure photosynthetic pigments. Fresh leaf (0.1g) was mixed in 80% acetone having a volume of 5 milliliters. The absorbance was observed with the help of ultraviolet-visible spectrophotometer at a wavelength of 645, 480, and 663 nm.

Antioxidants

A pre-chilled mortar and pestle was utilized to grind fresh leaves (0.5 g) in buffer solution (10 mL) having pH 7.8. After homogenization, the liquid was centrifuged for 20 minutes at 12,000 rpm. The supernatant with enzymatic antioxidants was collected and stored at -20°C for subsequent analysis of peroxidase, catalase, and superoxide dismutase activity based on protein content. The catalase activity was determined using the method ascribed by Chance and Maehly (1955). The peroxidase estimation was conducted following the Chance and Maehly (1955) method. The activity of superoxide dismutase was determined using the technique described by Giannopolitis and Ries (1977).

Reactive oxygen species

The H_2O_2 was assessed using the protocol described by Velikova *et al.* (2000). The malondialdehyde content was assessed using the method followed by Heath and Packer (1968).

Secondary metabolites

Total phenolic were calculated following the technique used by Julkunen-Tiitto (1985). The total alkaloid content was determined using the method outlined by Singh and Sahu (2006). The flavonoid content was assessed using the method developed by Zhishen *et al.* (1999). Riboflavin was extracted using the technique described by Okwu and Josiah (2006).

Gas exchange attributes

Attributes related to gas exchange were assessed with the help of a transferable infrared gas analyzer (LCA – 4 ACD, Hoddesdon, UK). A fully exposed and mature third leaf from each treatment group was randomly chosen for data collection. Measurements were taken between 12:00 and 14:00 hours on the respective day.

Statistical analysis

A complete block design (CRD) under a factorial arrangement with three replications was used. The analysis and evaluation of data were done by using a statistical package (Statistics 8.1). HSD test was used to compare the treatment means.

Results and Discussion

Growth attributes

Data depicted in Table 1 showed that root length (RL), shoot length (SL), root fresh weight (RFW), root dry weight (RDW), shoot fresh weight (SFW), and shoot dry weight (SDW) varied significantly ($P \leq 0.05$) in both varieties, salinity stress and seed priming treatments but, interaction between them was non-signifcant ($P > 0.05$) differences. Salinity stress resulted in reduced root length in both varieties but, the seed priming with 150 mM thiourea improved the RL up to 20.06% and 27.13% in TS-5 and TH-6 varieties, respectively. Salinity conditions decreased the SL of both varieties. However, seed priming with thiourea increased the SL 19.26% (TS-5) and 12.63% (TH-6) when compared with their respective controls. Salinity condition decreased the RFW of both varieties, but, the seed priming with 150 mM thiourea increased the RFW up to 49.01% and 28.47% in TS-5 and TH-6 varieties, respectively, when compared with their respective controls. Saline strress decreased the RDW of both varieties however, the seed priming with thiourea increased the RDW up to 98.59%

Table 1: *Influence of seed priming of thiourea on growth parameters of sesame varieties under saline conditions.*

Treatments	RDW (cm)	SL (cm)	RFW (cm)	RL (cm)	SDW (g)	SFW (g)
Salinity treatments (ST)						
Normal conditions (NC)	0.79 A	65.32 A	3.94 A	14.43 A	3.96 A	23.65 A
Saline conditions (SC)	0.28 B	46.66 B	2.25 B	10.78 B	2.66 B	16.92 B
Varieties (Vr)						
TS-5	0.39 B	51.91 B	2.34 B	11.39 B	3.04 B	17.9 B
TH-6	0.69 A	60.06 A	3.85 A	13.81 A	3.58 A	22.67 A
Seed Priming (SP)						
Hyrdo priming (HP)	0.47 B	52.43 B	2.63 B	11.39 B	2.97 B	18.81 B
Thiourea priming (TP)	0.6106 A	59.54 A	3.55 A	13.81 A	3.65 A	21.76 A
ST×Vr						
NC×TS-5	0.65 b	58.89 b	3.09 b	14.08 ab	3.69 a	22.13 ab
NC×TH-6	0.93 a	71.75 a	4.7875 a	14.77 a	4.22 a	25.17 a
SC×TS-5	0.13 d	44.95 c	1.57 c	9.71 c	2.38 b	13.75 c
SC×TH-6	0.44 c	48.37 c	2.91 b	11.84 bc	2.94 b	20.16 b
ST×SP						
NC×HP	0.70 a	61.63 a	3.38 b	13.16 b	3.54 b	21.87 a
NC× TP	0.88c	69.01 a	4.50 a	15.69 a	4.36 a	25.43 a
SC×HP	0.2369 b	43.25 b	1.88 d	9.63 c	2.39 c	15.75 b
SC×TP	0.33 b	50.07 b	2.61 c	11.92 bc	2.94 bc	18.08 b
Vr×SP						
TS-5×TP	0.48 bc	55.96 ab	2.76 b	12.89 ab	3.37 ab	18.93 bc
TH-6× HP	0.63 ab	57.00 a	3.36 b	11.89 b	3.23 ab	20.75 b
TS-5×HP	0.31 c	47.87 c	1.91 c	10.89 b	2.70 b	16.87 c
TH-6×TP	0.74 a	63.13 a	4.34 a	14.73 a	3.93 a	24.59 a
ST×Vr×SP						
NC×TS-5×HP	0.52 ns	54.7 ns	2.55 ns	12.97 ns	3.28 ns	21.14 ns
NC×TS-5×TP	0.78 ns	63.0 ns	3.64 ns	15.19 ns	4.11 ns	23.13 ns
SC×TS-5×HP	0.08 ns	41.0 ns	1.26 ns	8.82 ns	2.12 ns	12.61 ns
SC×TS-5×TP	0.17 ns	48.9 ns	1.88 ns	10.59 ns	2.64 ns	14.72 ns
NC×TH-6×HP	0.87 ns	68.5 ns	4.21 ns	13.35 ns	3.81 ns	22.61 ns
NC×TH-6×TP	0.99 ns	75.0 ns	5.36 ns	16.2 ns	4.63 ns	27.74 ns
SC×TH-6×HP	0.38 ns	45.5 ns	2.50 ns	10.43 ns	2.65 ns	18.88 ns
SC×TH-6×TP	0.48 ns	51.2 ns	3.33 ns	13.26 ns	3.24 ns	21.44 ns
Significance						
ST	0.000**	0.000**	0.000**	0.000**	0.000**	0.000**
SP	0.025*	0.002**	0.000**	0.001**	0.001**	0.003**
Vr	0.0000**	0.001**	0.000**	0.032*	0.007**	0.000**
ST× SP	0.411ns	0.89ns	0.276ns	0.854ns	0.468ns	0.506ns
ST× Vr	0.785ns	0.06ns	0.336ns	0.260ns	0.935ns	0.071ns
Vr×SP	0.564ns	0.64ns	0.713ns	0.507ns	0.943ns	0.335ns
ST× SP×Vr	0.469ns	0.96ns	0.835ns	0.863ns	0.913ns	0.467ns

*ST, Salinity treatments, NC, normal conditions, SC, saline conditions, Vr, Varieties, SP, Seed Priming, HP, Hyrdo priming, TP, Thiourea priming. * depicted significant ($p < 0.05$), ns depicted non significant ($p > 0.05$).*

and 26.94% in TS-5 and TH-6 varieties, respectively, when compared with their respective controls. Salinity stress resulted in decrease in the SFW of both varieties. But, the seed priming with 150 mM thiourea increased the SFW up to 16.70% and 13.52% in TS-5 and TH-6 varieties, respectively. Salinity decreased the SDW of both varieties, though, the seed priming with 150 mM thiourea improved the SDW up to 24.20% and 21.93% in TS-5 and TH-6 varieties, respectively, when compared with their respective controls.

Table 2: *Influence of seed priming of thiourea on growth parameters of sesame varieties under saline conditions.*

Treatments	Shoot Na^+ (mg/g d.wt.)	Root Na^+ (mg/g d.wt.)	Root K^+ (mg/g d.wt.)	Shoot K^+ (mg/g d.wt.)	Root Ca^+ (mg/g d.wt.)	Shoot Ca^+ (mg/g d.wt.)
Salinity treatments (ST)						
Normal conditions (NC)	4.34 B	10.75 B	9.56 A	15.34 A	8.56 A	12.59 A
Saline conditions (SC)	5.65 A	14.71 A	7.13 B	10.719 B	5.7187 B	8.563 B
Varieties (Vr)						
TS-5	4.84 A	11.93 B	8.06 A	13.46 A	5.78 B	9.46 B
TH-6	5.15 A	13.53 A	8.62 A	12.59 A	8.5 A	11.688 A
Seed priming (SP)						
Hyrdo priming (HP)	5.46 A	13.81 A	7.59 B	11.93 B	6.41 B	9.25 B
Thiourea priming (TP)	4.53 B	11.65 B	9.09 A	14.12 A	7.87 A	11.91 A
ST×Vr						
NC×TS-5	4.5 bc	10.87 c	8.37 c	15.5 a	7.43 b	12.18 ab
NC×TH-6	4.18 c	10.62 c	10.75 a	15.18 a	9.68 a	13.0 a
SC×TS-5	5.18 b	13.0 b	7.75 b	11.43 b	4.12 c	6.75 c
SC×TH-6	6.12 a	16.43 a	6.5 b	10.0 b	7.31 b	10.37 b
ST×SP						
NC×HP	4.75 b	11.87 b	8.68 ab	14.43 ab	7.43 b	10.37 b
NC× TP	3.94 c	9.62 c	10.43 a	16.25 a	9.68 a	14.81 a
SC×HP	6.18 a	15.75 a	6.50 c	9.43 c	5.37 b	8.12 b
SC×TP	5.12 b	13.68 b	7.75 bc	12.0 bc	6.06 b	9.0 b
Vr×SP						
TS-5×HP	5.50 a	13.12 a	6.93 b	12.00 a	5.31 c	8.62 b
TH-6× TP	4.87 ab	12.6 ab	9.0 ab	13.31 a	9.5 a	13.5 a
TS-5×TP	4.18 b	10.75 b	9.18 a	14.93 a	6.25 bc	10.31 b
TH-6×HP	5.43 a	14.5 a	8.25 ab	11.87 a	7.50 ab	9.87 b
ST×Vr×SP						
NC×TS-5×HP	5.25 ns	12.3 ns	7.12 ns	14.87 ns	6.87 ns	10.75 ns
NC×TS-5×TP	3.75 ns	9.5 ns	9.62 ns	16.12 ns	8.00 ns	13.62 ns
SC×TS-5×HP	5.75 ns	14.0 ns	6.75 ns	9.12 ns	3.75 ns	6.50 ns
SC×TS-5×TP	4.62 ns	12.0 ns	8.75 ns	13.75 ns	4.5 ns	7.0 ns
NC×TH-6×HP	4.25 ns	11.5 ns	10.25 ns	14.0 ns	8.0 ns	10.0 ns
NC×TH-6×TP	4.12 ns	9.75 ns	11.25 ns	16.37 ns	11.37 ns	16.0 ns
SC×TH-6×HP	6.62 ns	17.5 ns	6.25 ns	9.75 ns	7.0 ns	9.75 ns
SC×TH-6×TP	5.62 ns	15.4 ns	6.75 ns	10.25 ns	7.62 ns	11.0 ns
Significance						
ST	0.000**	0.000**	0.000**	0.000**	0.000**	0.000**
SP	0.000**	0.000**	0.009**	0.021*	0.021*	0.000**
Vr	0.02*	0.005**	0.298ns	0.313ns	0.000**	0.001**
ST× SP	0.526ns	0.85ns	0.641ns	0.662ns	0.170ns	0.09ns
ST× Vr	0.07ns	0.06ns	0.07ns	0.514ns	0.405ns	0.04ns
Vr×SP	0.065ns	0.68ns	0.169ns	0.386ns	0.346ns	0.139ns
ST× SP×Vr	0.121ns	0.59ns	1.000ns	0.135ns	0.294ns	0.358ns

ST, Salinity treatments, NC, normal conditions, SC, saline conditions, Vr, Varieties, SP, Seed Priming, HP, Hyrdo priming, TP, Thiourea priming.

Ions

The shoot and root Na^+, K^+ and Ca^{2+} content varied significantly ($P \leq 0.05$) in both varieties, salinity and seed priming, whereas the interaction between them was found to be non-significant (Table 2). Salinity stress enhanced the shoot Na^+ of both varieties however, the seed priming with 150 mM thiourea decreased the shoot Na^+ up to 19.56% and 15.09% in TS-5 and TH-6 varieties respectively when compared with their respective controls. Salinity

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boosted the root Na^+ in both varieties. However, the seed priming with 150 mM thiourea reduced the root Na^+ up to 14.28% and 12.14% in TS-5 and TH-6 varieties, respectively, when compared with their respective controls. Overall, TH-6 variety performed better when compared with TS-5 variety. Salinity stress decreased the K^+ ions in root in both varieties. However, the seed priming with 150 mM thiourea increased the K^+ ions in root up to 29.62% and 8% in TS-5 and TH-6 varieties, respectively, when compared with their respective controls. Overall, TH-6 variety performed better when compared with TS-5 variety. Salinity decreased the K^+ ions in shoot in TS-5 (38.65%) and in TH-6 (30.35%), moreover, the seed priming with thiourea improved the shoot K^+ up to 50.68% and 5.13% in TS-5 and TH-6 varieties, respectively, when compared with their respective controls. Salinity decreased the root Ca^{2+} in both varieties moreover the seed priming with 150 mM thiourea increased the root Ca^{2+} 20% (TS-5) and 8.92% (TH-6) when compared with their respective controls. Salinity stress decreased the shoot Ca^{2+} in both varieties; moreover, the seed priming with 150 mM thiourea increased the shoot Ca^{2+} by 7.69% (TS-5) and 12.82% (TH-6).

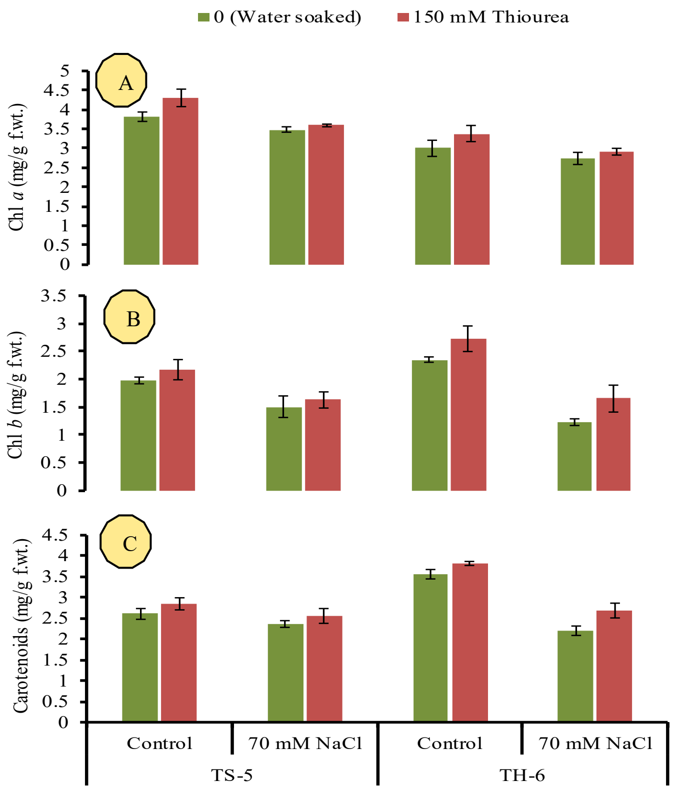

Figure 1: *Effect of thiourea seed priming on photosynthetic pigments of Sesame plant under salinity stress.*

Photosynthetic pigments

The chlorophyll a content varied significantly ($P \leq 0.05$) in both varieties, salinity stress, and seed priming, although the interaction between them depicted non-significant ($P > 0.05$) differences expect carotenoids (Figure 1; Table 3). Salt stress decreased the chlorophyll a content of both varieties; though, the seed priming with 150 mM thiourea increased the chl *a* 3.59% (TS-5) and 5.45% (TH-6) when compared with respective controls. Salinity stress reduced the contents of chlorophyll b in both varieties; however, the seed priming with 150 mM thiourea improved the chlorophyll b up to 8.33% and 34.69% in TS-5 and TH-6 varieties, respectively, when compared with their respective controls. Overall, TH-6 variety performed better when compared with TS-5 variety. Salinity stress decreased the carotenoids contents of both varieties, however, the seed priming with 150 mM thiourea increased the carotenoids 8.51% (TS-5) and 21.86% (TH-6) when compared with respective controls.

Table 3: *Influence of Seed priming of thiourea on photosynthetic pigments of sesame varieties under saline conditions.*

Significance	Chl a (mg/g f.wt.)	Chl b (mg/g f.wt.)	CAR (mg/g f.wt.)
ST	0.000**	0.000**	0.000**
SP	0.02*	0.021*	0.004**
Vr	0.000**	0.150ns	0.000**
ST×SP	0.182ns	0.956ns	0.683ns
ST× Vr	0.498ns	0.08ns	0.06ns
Vr×SP	0.821ns	0.306ns	0.424ns
ST× SP×Vr	0.734ns	0.786ns	0.503ns

ST, Salinity treatments, NC, normal conditions, SC, saline conditions, Vr, Varieties, SP, Seed Priming, HP, Hyrdo priming, TP, Thiourea priming.

Oxidative stress

Statistical results for malondialdehyde and hydrogen peroxide revealed that salt stress and cultivars and seed priming had significant differences but the interaction among them was non-significant ($P > 0.05$) (Figure 2A; Table 4). Salinity stress increased the MDA of both varieties; however, the thiourea seed priming decreased the MDA up to 20.68% and 14.01% in TS-5 and TH-6, respectively, when compared with their respective controls. Salinity stress increased the hydrogen peroxide of both varieties by 63.51% (TS-5) and 10.45% (TH-6) as compared to controls; however, the seed priming with 150 mM thiourea decreased the hydrogen peroxide up to 25.26% and 23.08 % in TS-5 and TH-6 varieties, respectively.

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Table 4: *Influence of Seed priming of thiourea on photosynthetic pigments of sesame varieties under saline conditions.*

Significance	SOD (units mg^{-1} protein)	POD (units mg^{-1} protein)	CAT (units mg^{-1} protein)	H_2O_2 (μmolg^{-1} f.wt.)	MDA (mmolg^{-1} f.wt.)
ST	0.000**	0.000**	0.000**	0.000**	0.005**
SP	0.000**	0.025*	0.000**	0.000**	0.008**
Vr	0.761ns	0.003**	0.135ns	0.005**	0.012**
ST×SP	0.137ns	0.276ns	0.984ns	0.638ns	0.983ns
ST× Vr	0.062ns	0.929ns	0.921ns	0.063ns	0.264ns
Vr×SP	0.389ns	0.359ns	0.766ns	0.237ns	0.278ns
ST× SP×Vr	0.061ns	0.976ns	0.539ns	0.073ns	0.871ns

ST, Salinity treatments, NC, normal conditions, SC, saline conditions, Vr, Varieties, SP, Seed Priming, HP, Hyrdo priming, TP, Thiourea priming.

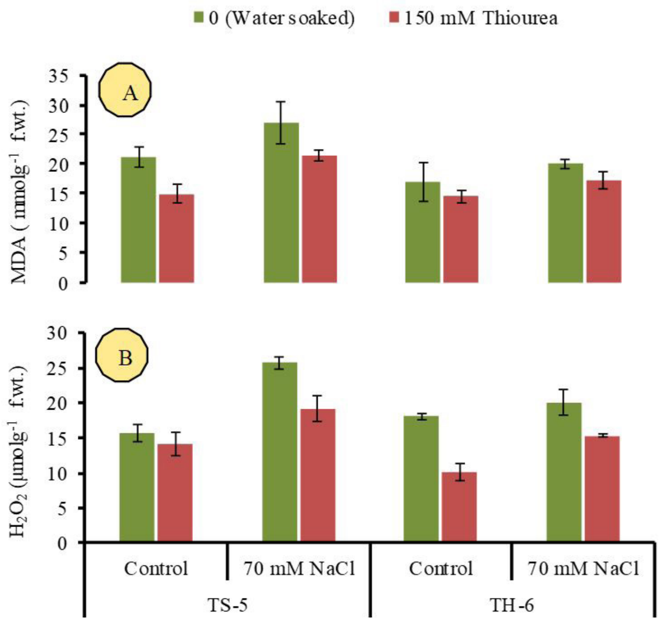

Figure 2: *Effect of thiourea seed priming on reactive oxygen species in sesame under salinity stress.*

Antioxidants

The SOD, POD, CAT varied significantly (P≤0.05) in salinity stress, seed priming, and varieties while the interaction among them was non-significant (P>0.05) differences (Figure 3A; Table 4). Salinity stress increased the SOD of both varieties. Likewise, the seed priming 150 mM thiourea also increased the SOD up to 7.57% (TS-5) and 38.32% (TH-6) as compared to their respective controls. Salinity stress increased this attribute by 14.41 and 17.15% respectively as compared to control plants. Salinity stress increased the CAT of both varieties. Moreover, the seed priming with 150 mM thiourea also increased the CAT upto 14.14% and 17.51% in TS-5 and TH-6, respectively, as compared to their respective controls.

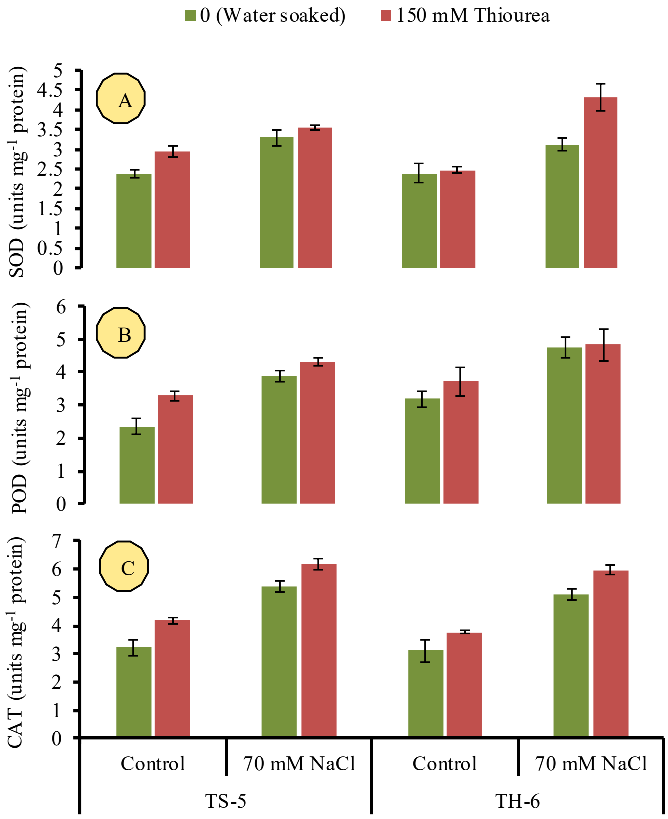

Figure 3: *Effect of thiourea seed priming on enzymatic antioxidant in sesame under salinity stress.*

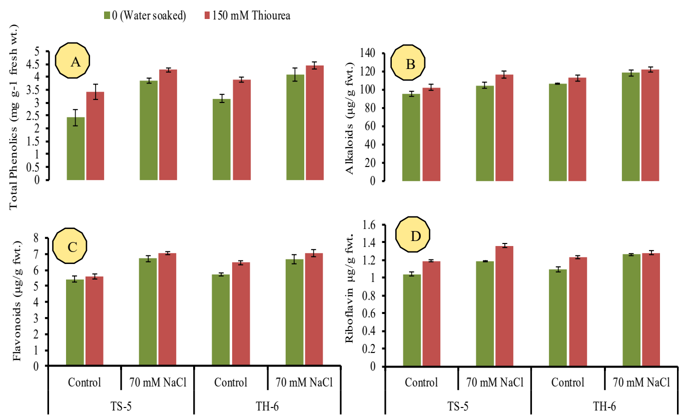

Figure 4: *Effect of thiourea seed priming on osmolytes and secondary metabolites in sesame under salinity stress.*

Secondary metabolites

Statistical data presenting total phenolics, alkaloids, flavonoids, and riboflavin, salinity stress, seed priming, and varieties displayed significant (P≤0.05) differences, however, the interaction was found to be non-significant (P>0.05) difference (Figure 4A; Table 5). Salt stress increased the total phenolics of both varieties; likewise, the seed priming also increased the total phenolics up to 11.03% and 8.53% in TS-5 and TH-6 varieties, respectively, when compared with their respective controls. Salinity stress increased the alkaloids of both varieties and the seed priming also increased alkaloids up to 10% and 3.28%, in TS-5 and TH-6 varieties, respectively, when compared with their respective controls. Salinity stress increased the flavonoids in both varieties and the seed priming also increased flavonoids upto 4.83% (TS-5) and 5.83% (TH-6), when compared with their respective controls. Salinity stress increased the riboflavin of both varieties and the seed priming with thiourea also increased riboflavin up to 14.81% and 1.45% in TS-5 and TH-6 varieties respectively, when compared with their respective controls.

Table 5: *Influence of Seed priming of thiourea on secondary metabolites of sesame varieties under saline conditions.*

Significance	Total soluble phenolics	Alkaloids	Flavo-noids	Ribofla-vin
	(mg g-1 fresh wt.)	(µg/g fwt.)	(µg/g fwt.)	(µg/g fwt.)
ST	0.000**	0.000**	0.000**	0.000**
SP	0.000**	0.003**	0.004**	0.000**
Vr	0.008**	0.0001**	0.029*	0.108ns
ST×SP	0.111ns	0.872ns	0.686ns	0.103ns
ST× Vr	0.17ns	0.827ns	0.064ns	0.085ns
Vr×SP	0.55ns	0.329ns	0.223ns	0.08ns
ST× SP×Vr	0.74ns	0.458ns	0.278ns	0.06ns

ST, Salinity treatments, NC, normal conditions, SC, saline conditions, Vr, Varieties, SP, Seed Priming, HP, Hyrdo priming, TP, Thiourea priming.

Gas exchange attributes

The photosynthetic rate, Ci, gs, and Tr varied significantly (P≤0.05) in varieties, salinity stress and seed priming, while the interaction among them was non-significant (P>0.05) differences (Figure 5A; Table 6). Salinity stress decreased the photosynthetic activity upto 41.8% (TS-5) and 51.14% (TH-6) of both varieties. Moreover, the seed priming with 150 mM thiourea also increased the photosynthetic activity upto 47.88% and 48.23% in TS-5 and TH-6, respectively, as compared to their respective controls. Salinity stress increased the Ci of both varieties however, the seed priming with 150 mM thiourea decreased the Ci up to 16.10% and 12.84% in TS-5 and TH-6 varieties, respectively. Salt stress reduced the Stomatal conductivity in both varieties; conversely, the seed priming increased Stomatal conductivity up to 6.10% (TS-5) and 13.73% (TH-6), when compared with their respective controls. Salinity stress decreased the transpiration rate in both varieties but the seed priming with 150 mM thiourea increased transpiration rate up to 54.74% and 34.16%, in TS-5 and TH-6 varieties, respectively, when compared with their respective controls.

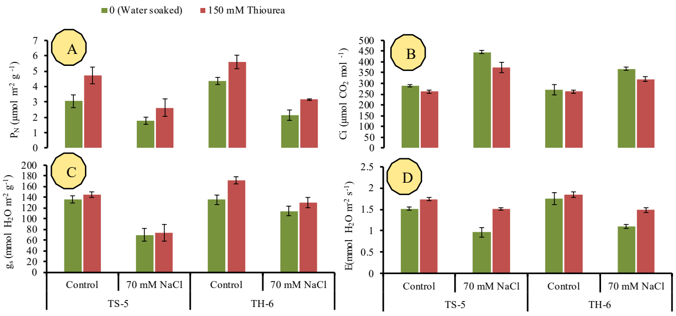

Figure 5: *Effect of thiourea seed priming on gaseous exchange attributes in sesame under salinity stress.*

Table 6: *Influence of Seed priming of thiourea on gas exchange parameters of sesame varieties under saline conditions.*

Significance	gs	PN	E	Ci
	(mmol H_2O m^{-2}g^{-1})	(µmol m^{-2} g^{-1})	(mmol H_2O m^{-2}s^{-1})	(µmol CO_2 mol^{-1})
ST	0.000**	0.000**	0.000**	0.000**
SP	0.026*	0.000**	0.000**	0.000**
Vr	0.000**	0.011**	0.034*	0.000**
ST×SP	0.366ns	0.349ns	0.09ns	0.08ns
ST× Vr	0.80ns	0.249ns	0.268ns	0.06ns
Vr×SP	0.178ns	0.822ns	0.182ns	0.268ns
ST× SP×Vr	0.582ns	0.591ns	0.919ns	0.869ns

ST, Salinity treatments, NC, normal conditions, SC, saline conditions, Vr, Varieties, SP, Seed Priming, HP, Hyrdo priming, TP, Thiourea priming.

Plants response under stress conditions is to employ their potential to advance the defense mechanism instead of productivity (Zhang *et al*., 2023). Likewise salinity stress also negatively affected the mechanisms in plants and ultimately reduced growth (Dabravolski and Isayenkov, 2023). It also negatively exaggerated the root and shoot lengths, root fresh and dry weight (Table 1), this research was supported by Nikfekr *et al*. (2023) and Dangue *et al*. (2022). Similar reduction was observed in various other crops such as maize (Sabagh *et al*., 2021; Ali *et al*., 2023), wheat (Hmissi *et al*., 2023), sorghum (Kaur *et al*., 2023) and coriander (Vojodi-Mehrabani and Kheirollahi, 2023; Sánchez-Navarro *et al*., 2024). Thiourea could effectively alleviate the adverse effects of salt stress and toxicities (Yadav *et al*., 2023), for example, thiourea application increased the growth and physiological attributes of mustard (Saleem *et al*., 2024), enhanced the antioxidant enzymes and decreased reactive oxygen species

(Ahmad *et al.*, 2023; Fiaz *et al.*, 2024). The mechanism for stress mitigating effects of TU applications either foliar or seed priming have been investigated at physiological and molecular levels. Thiourea mainly controls the redox equilibrium mechanism in a cellular environment under stress (Patade *et al.*, 2020).

Thiourea (TU) is increasingly being studied as a bioregulator for crop plant growth and development (Ahmad *et al.*, 2022b). TU seed priming increased the root and shoot lengths, root fresh and dry weight of sesame varieties, however, TH-6 showed better growth indicators than TS-5 (Table 1), Exogenous administration of TU increases plant growth and productivity in both normal and stressful conditions (Zahra *et al.*, 2022b). Previous research has demonstrated the benefits of exogenous TU application as a priming agent for seed pretreatment, foliar spray, and medium supplement for a variety of crop species. The use of TU has been shown to improve plant tolerance to a variety of environmental stresses, including salinity, heat, heavy metals, and drought (Granaz *et al.*, 2022; Harisha *et al.*, 2023; Zahid *et al.*, 2024).

Salinity stress negatively impacts the photosynthetic machinery and causes irreparable damage to it at any developmental stage. Photosynthesis is essential for the survival of all organisms and is a major factor in plant productivity by creating all precursor biomolecules. Both varieties TS-5 and TH-6, photosynthetic pigments (Chl a, Chl b, and carotenoids) were decreased under salinity, however, seed priming with thiourea improved photosynthetic pigments (Figure 1). The present study outcomes corroborate with the results of Saddiq *et al.* (2021), Shahid *et al.* (2023), and Lalarukh *et al.* (2023). Under salinity stress, a significant decrease in photosynthetic content was observed; this could be because salinity stress negatively affects leaf anatomy, chloroplast ultrastructure and metabolism (Hameed *et al.*, 2021; Barhoumi *et al.*, 2022). Moreover, salinity stress decreased the gas exchange indicators like transpiration rate, photosynthetic rate and stomatal conductance while increased the sub-stomatal CO_2 level (Figure 1). Lower gas exchange characteristics under salinity stress may be associated with increased ROS generation, which closes the stomata while thiourea application decreased the production of abscisic acid and controls the ROS induced stomatal closure (Sahoo *et al.*, 2023).

Oxidative stress is one of the most promising effects on plants resulting in the reactive oxygen species production, causing the cellular compartments degradation and inhibition of their functions (Hasanuzzaman *et al.*, 2021; Zahra *et al.*, 2021). However, there is noteworthy inter and intraspecific variance in production of ROS and also tolerance against salinity stress. In the current study, there was a significant increase in the production of H_2O_2 and MDA under saline conditions while the seed priming with thiourea proved helpful to limit their production in both normal and saline conditions (Figure 4). Moreover, higher H_2O_2 and MDA production was noted in TH-5 than TS-6. Among various harmful ions the Na^+ and Cl^- were proved particularly to be more damaging in terms of plants cellular membranes (Khare *et al.*, 2020). These ions move taken up by roots and transported to other plant bodies causing additional damage. Impairment to cellular structures results in the increase in the production of ROS, and in different reactive species H_2O_2 is the most damaging and longer half-life (Dumanović *et al.*, 2021). In salinity stress, the production of antioxidants assists the plants to overcome the adverse oxidative stress (Ahmad *et al.*, 2019). Sesame priming with thiourea under saline conditions exhibited higher activities of POD, CAT and SOD (Figure 5). Fiaz *et al.* (2024) noted that the application of thiourea enhanced the activity of SOD, CAT and POD and reduced the level of MDA and H_2O_2. The results of the current trial were similar with the outcomes of Nouman and Aziz (2022) which depicted that seed priming of thiourea the increased activity of SOD, CAT, POD, riboflavin, flavonoids, and alkaloids in *Calotropis procera*. Salinity stress increased total phenolics, flavonoids, riboflavin and alkaloids in both varieties. Moreover, thiourea seed priming also improved these secondary metabolites under saline and control conditions (Figure 2). Zhang *et al.* (2017) reported that amino acid and carbohydrate metabolic pathways significantly improved in the adaption to salinity stress. In current experiment, the total phenolics, flavonoids, riboflavin and alkaloids enhanced under salinity stress was comarable in sugar beet (El-Mageed *et al.*, 2022), maize (Shahid *et al.*, 2023) and sunflower (Barros *et al.*, 2019). Salinity stress resulted in the increase of Na^+ ions in both root and shoot while resulted in a decrease in the Ca^{2+} and K^+, while the thiourea treatment decreased the accumulation of Na^+ ions and increased the K^+ and Ca^{2+} ions (Table 2). High salinity results in disturbance of K^+ ions cytosolic homeostasis and plants endurance, which are deliberates the most essential salt tolerance mechanisms in plants, resulting in significant K^+ efflux and Na^+ buildup (Abbasi *et al*., 2014). In the current trial, salinity-stressed plants mount up more Na^+ and less K^+ than control sesame plants, this could be the consequence of potential antagonism between K^+ and Na^+ (Ferreira *et al*., 2020).

Conclusions and Recommendations

Salinity is the major threat to the growth of sesame. Salinity decreases the photosynthetic pigments and efficiency, impairs the balance between antioxidants and oxidants, and lessens the uptake of essential minerals irrespective of varietal differences. However, the performance of TH-6 was better than TS-5. In addition, the seed priming of thiourea enhanced the sesame photosynthetic pigments and efficiency, secondary metabolites production, antioxidant machinery, and nutrient uptake in both varieties which increased growth and development as a result. So, thiourea seed priming is an effective strategy to counteract the negative effects of salt stress by improving tolerance mechanisms.

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Novelty Statement

Priming seeds with thiourea offers a promising approach to mitigate the detrimental effects of salt stress by enhancing tolerance mechanisms.

Author's Contribution

Bushra Irfan: Conducted the experiment and data collection.
Muhammad Shahzad: Supervised the experiment as Project Head.
Asif Mukhtiar: Data collection
Muhammad Zubair Akram: Initial drafting and finalizing the MS.
Muhammad Atif Bashir: Statistical analysis.
Sabina Asghar: Helped in relevant literature.
Abdul Ghaffar and Samreen Nazeer: Reviewed final draft of the MS.

Conflict of interest

The authors have declared no conflict of interest.

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