Silicon
https://doi.org/10.1007/s12633-025-03591-2

RESEARCH

Enhancement of Physio-Biochemical Attributes and Seed Yield of Sunflower Through Integrated Application of Silicon and Mycorrhizal Fungi Under Salt Stress

Md. Shariful Islam[1] · Md. Asadur Rahman[1] · Mst. Sabiha Sultana[1] · Md. Monirul Islam[1] · Milton Halder[2] · Debesh Das[1]

Received: 10 June 2025 / Accepted: 25 December 2025

Abstract
Salinity is a predominant abiotic stressor that severely impairs agricultural productivity by disrupting plant physiological and biochemical processes. The strategic application of silicon (Si) fertilizer in conjunction with arbuscular mycorrhizal fungi (AMF) has emerged as a promising approach to alleviate the detrimental impacts of salinity stress in sunflower. The present study was conducted to assess the synergistic effects of monosilicic acid and AMF inoculation on the growth performance, physiological attributes, and seed yield of sunflower under varying levels of salt stress. A factorial experiment was arranged in a completely randomized design (CRD) with three replicates, comprising three factors: (1) four monosilicic acid application rates (0 [Si_0], 150 [Si_{150}], 300 [Si_{300}], and 450 [Si_{450}] kg ha^{-1}), (2) four irrigation water salinity levels (0.54 [control], 4, 8, and 12 dS m^{-1}), and (3) two AMF inoculation treatments (absence [–AMF] and presence [+ AMF]). Salinity stress significantly reduced all measured growth indices, physiological traits, and seed yield of sunflower but Si supplementation notably enhanced physio-biochemical traits and stress tolerance index. It has been reported that, Si-treated plants improved leaf relative water content by 45%, chlorophyll content (SPAD value) by 17%, and membrane stability index by 60%, along with a 15% reduction in electrolyte leakage, relative to untreated controls at 12 dS m^{-1} salinity level. Moreover, the highest accumulation of proline, was recorded in plants treated with Si_{450}, with increases of 19% and 28% observed in AMF-inoculated and non-inoculated plants, respectively, compared to the non-saline control. AMF inoculation significantly enhanced reproductive output, with increases of 23% in capitulum (head) weight and 41% in seed number per plant compared to non-inoculated counterparts. Under high salinity (12 dS m^{-1}), Si_{450} treatment led to a substantial increase in seed yield by 56% in + AMF plants and 50% in –AMF plants relative to the Si_0 treatment. Collectively, the findings suggest that the integrated application of Si and AMF markedly augments morpho-physiological performance and seed yield of sunflower through mitigating the adverse effects of salt-induced stress.

Keywords Sunflower · Salt stress · Silicon · AMF · Proline content · Seed yield

1 Introduction

Soil salinity is a critical ecological constraint to global agricultural productivity, a challenge that is further exacerbated by climate change, sea level rise, and unsustainable agricultural practices. Salinity stress adversely affects a range of physiological and biochemical processes in crop plants, including photosynthesis, transpiration, stomatal conductance, and assimilate translocation, all of which are intricately linked to crop performance and yield [1, 2]. The progressive accumulation of salts in the rhizosphere leads to a decline in soil fertility and productivity, thereby necessitating the development of salt-tolerant genotypes or the enhancement of plant resilience to salinity stress [3, 4]. In this context, sustainable nutrient management strategies are gaining prominent opportunity to preserve soil health, fertility, and ensure agricultural sustainability. So, combined application of arbuscular mycorrhizal fungi (AMF) and silicon (Si) is a promising agronomic approach for improving morpho-physiological traits, seed yield, and stress tolerance

✉ Debesh Das
debeshdasat@at.ku.ac.bd

[1] Agrotechnology Discipline, Khulna University, Khulna 9208, Bangladesh

[2] Soil, Water and Environment Discipline, Khulna University, Khulna 9208, Bangladesh

Published online: 08 January 2026

in sunflower (*Helianthus annuus* L.), which is a popular oilseed crop that consisted of proteins, lipids, fatty acids, and bioactive phytochemicals with moderate salt tolerance.

Silicon (Si), the second most abundant element in the lithosphere following oxygen, comprises approximately 29% of the Earth's crust, primarily existing in the inert form of silicon dioxide (SiO_2), which is not directly bio-available to plants. Plants assimilate Si exclusively as monosilicic acid [$Si(OH)_4$], the soluble and phytoavailable form present in the soil solution at low concentrations [5]. Although not classified as an essential nutrient, Si confers substantial agronomic benefits by enhancing plant resilience to a range of abiotic stressors. Its role in stress mitigation is attributed to improved root hydraulic conductance, augmented water and nutrient uptake, enhanced photosynthetic efficiency, optimized stomatal regulation, improved leaf water status, and activation of the antioxidative defense system [5, 6]. Under salinity stress, Si-enriched plants exhibit superior osmotic adjustment, decreased stomatal conductance, and improved leaf–water relations, resulting in enhanced tolerance to ionic and osmotic perturbations [7, 8]. The physiological and biochemical mechanisms underlying Si-mediated stress alleviation include elevated root hydraulic conductivity, improved water-use efficiency, enhanced macronutrient and micronutrient acquisition, and stabilization of photochemical processes [6, 9]. Increased Si availability promotes robust root system architecture by enhancing root elongation, lateral root density, and root biomass accumulation, thereby improving mechanical tissue strength and overall plant vigor under stress conditions [10, 11]. Silicon also exerts a positive influence on seed germination, plasma membrane integrity, carbon assimilation, plant–water homeostasis, phytohormonal regulation, and nutrient uptake dynamics [12, 13]. A critical structural role of Si involves the formation of a cuticle–silica double layer beneath the leaf epidermis, which significantly curtails transpirational water loss under salinity stress.

Arbuscular mycorrhizal fungi (AMF) play a pivotal role in advancing sustainable agricultural systems by functioning as effective biofertilizers that enhance plant resilience to a wide range of environmental stressors [14]. These symbiotic fungi form a mutualistic associations with the roots of most terrestrial plants, wherein the host plant supplies carbon to the fungi, and in return, AMF facilitate the acquisition of essential nutrients—such as phosphorus (P), zinc (Zn), and copper (Cu) from beyond the rhizosphere via an extensive network of extra-radical hyphae [15]. AMF have been widely recognized for their ability to alleviate the detrimental effects of abiotic stresses, particularly salinity, by enhancing stress tolerance mechanisms in host plants [16]. AMF significantly improve root system architecture by increasing root colonization, root length density, and the development of root hairs, thereby enabling deeper soil exploration for moisture and nutrient uptake [17]. This enhanced root-soil interface facilitates more efficient nutrient cycling and water acquisition, which is critical for optimal crop performance under suboptimal environmental conditions. Additionally, AMF contribute to stress mitigation by inducing the synthesis and accumulation of osmoprotectants and stress-related proteins that protect plant cells from oxidative damage induced by reactive oxygen species under saline conditions [18].

Moreover, AMF enhance soil biological activity by secreting extracellular enzymes that mediate organic matter decomposition, nutrient mineralization, and the biosynthesis of secondary metabolites, thereby strengthening plant-soil interactions and promoting rhizosphere health [19]. Their ability to reduce reliance on synthetic fertilizers makes them a key component in reducing the environmental footprint of conventional agriculture [20]. In addition, mycorrhizal colonization has been empirically demonstrated to enhance growth, morphological traits, and overall vigor in economically important crops such as sunflower (*Helianthus annuus* L.), thereby contributing to improved yield and resource use efficiency [21]. Collectively, AMF serve as a critical biological tool for improving crop productivity, enhancing stress resilience, and promoting agro-ecosystem sustainability. Exogenous application of Si and AMF significantly augmented morpho-physiological attributes, biochemical traits and yield of soyabean, sunflower [21]. It has been reported that co-application of Si and mycorrhizal fungi sows synergistic interaction on different field crops particularly sunflower. Nutrient dynamics in rhizosphere highly regulated by the combine application of silicon and mycorrhizal fungi.

In the light of aforementioned information, it became apparent that a large number of published literatures assessed the individual effect of AMF and Si on a variety of crops, but their combined effects on the growth, physiological characteristics, and yield of sunflower under salt stress were little bit explored. Therefore, the present study was aimed to investigate the ameliorative role of Si and AMF on morpho-physiological characteristics and seed yield of sunflower under salt stress.

2 Materials and Methods

2.1 Experimental Site

A pot experiment was carried out from January to May 2024 at the field laboratory of Professor Dr. Purnendu Gain, under the Agrotechnology Discipline at Khulna University, Bangladesh (22°48′ N; 89°32′ E). Following the harvest, a postharvest evaluation of the sunflower plants and heads was conducted at the Agronomy and Horticulture Laboratory, also within the Agrotechnology Discipline at Khulna

University, to assess various physicochemical quality parameters. The soil used for the experiment was collected from a farmer's field in Dumuria, Khulna, and its composition (Table 1) is detailed below.

2.2 Experimental Treatments and Design

A factorial experiment was conducted using a completely randomized design (CRD) with three replicates. The study involved three factors: (1) four application rates of monosilicic acid—0 (Si_0), 150 (Si_{150}), 300 (Si_{300}), and 450 (Si_{450}) kg ha^{-1}; (2) four levels of irrigation water salinity—0.54 (control), 4, 8, and 12 dS m^{-1}; and (3) two arbuscular mycorrhizal fungi (AMF) inoculation treatments: absence (–AMF) and presence (+ AMF) of mycorrhizal fungi.

$$\text{Total treatment combinatios} = \text{Monosilicic acid doses (4)} \times \text{Salinity levels (4)} \times \text{AMF inoculation (2)} \times \text{Replication (3)} = 96$$

Treatments were arranged in a factorial completely randomized design (CRD) with three replications in which each pot with single plant was considered as a treatment combination.

2.3 Crop Husbandry

Sunflower seeds were obtained from the Bangladesh Agricultural Research Institute (BARI), Gazipur. The seeds were surface sterilized using 10% hydrogen peroxide (H_2O_2) for 15 min, thoroughly rinsed with distilled water, soaked for 12 h, and then sown in earthen pots measuring 40 cm in height, 35 cm in top diameter, and 25 cm in bottom diameter. Each pot was filled with 13 kg of dry soil and fertilizers were applied following the standard recommendations outlined in the *Krishi Projukti Hatboi* published by BARI.

Table 1 Composition of soil sample

Soil composition	Value
Sand	22%
Silt	34%
Clay	44%
Field capacity	42%
Soil pH	7.1
Organic matter content	2.65%
Inherent salinity	0.54 dS m^{-1}
Total N	0.18%
Exchangeable P	0.0064%
Exchangeable K	0.039%
Exchangeable Ca	0.47%
Exchangeable Mg	0.052%

AMF inoculum, containing at least 25 spores of *Glomus* spp. per gram, was sourced from the Asian Institute of Technology (AIT), Thailand. To allow for initial establishment, the AMF inoculum was incorporated into the potted soil five days prior to seed sowing. Fourteen grams of inoculum (providing a minimum of 350 spores) were added to each pot. Control pots received an equivalent amount of autoclaved (non-viable) inoculum to ensure experimental consistency. In addition, monosilicic acid (MSA) was applied at four different rates—0, 150, 300, and 450 kg ha^{-1} by mixing it into the soil of the corresponding pots. The MSA used in this experiment contained approximately 21% silicon (Si), serving as the source of Si supplementation.

2.4 Imposition of Soil Salinity as Experimental Treatments

Commercial-grade sodium chloride (NaCl) was procured from the local market and dissolved in tap water to prepare saline solutions of varying electrical conductivities (EC). The desired salinity levels were achieved by calculating and adjusting the NaCl concentrations using a portable EC meter (Lutron CD-4301 Electronic Conductivity Meter, Taiwan). The intrinsic EC of the tap water (control) was 0.54 dS m^{-1}. To formulate solutions with target EC levels, 2.2 g, 4.3 g, and 6.8 g of NaCl were dissolved in 1 L of water to obtain salinity levels of 4 dS m^{-1}, 8 dS m^{-1}, and 12 dS m^{-1}, respectively [22]. Each pot received 500 mL of the designated saline solution weekly, beginning at the early vegetative stage (21 days after sowing) and continuing through the flowering stage (50 days after sowing). Thereafter, irrigation was continued using non-saline water as needed to maintain the soil at field capacity, ensuring optimal vegetative and reproductive development of sunflower plants.

2.5 Data Collection

2.5.1 Morphological, Physiological and Yield Attributes

Data were collected on a range of morphological, physiological, and yield-related parameters, including plant height (cm), stem diameter, root biomass (g $plant^{-1}$), shoot biomass (g $plant^{-1}$), leaf greenness (SPAD value), leaf relative water content (RWC, %), membrane stability index (MSI, %), electrolyte leakage (EL, %), proline concentration (µg g^{-1} fresh weight), head weight, head diameter, seed number, and seed yield (g $plant^{-1}$). Plant height was measured seven days prior to harvest, from the soil surface to the tip of the uppermost leaf. Root and shoot samples corresponding to each treatment combination were carefully excavated, washed to remove soil particles, and oven-dried at 72 °C for 36 h to determine root and shoot biomass. Just after cleaning, root

volume was measured by using the Archimedes principle for water displacement.

2.5.2 Physiological and Biochemical Traits

The measures a plant's relative leaf chlorophyll content (SPAD values) were noted using a portable chlorophyll meter (SPAD-502 Plus, Konica Minolta, Tokyo, Japan) during flowering period of the plants. Fully expanded leaves were randomly selected, and two SPAD values were measured from each experimental unit followed by average to obtain a representative reading for each experimental unit. Relative water content (RWC) is a measure of how much water is in a plant leaf compared to its maximum capacity. RWC was determined at the initial flowering stage using the method described by [23]. Initially, the topmost second leaves of the plants were collected and were weighed immediately to obtain their fresh weight. After that, each leaf was sliced into 2 cm segments and submerged into distilled water for 12 h to become fully turgid followed by measuring turgid weight. Then, fully turgid leaf segments were dehydrated in an oven at 72 °C for 36 h. Finally, RWC was measured using the following formula:

$$\text{RWC}\ (\%) = \frac{(\text{FW} - \text{DW})}{(\text{TW} - \text{DW})} \times 100 \quad (1)$$

Electrolyte leakage is the outflow of electrolyte from plant cell or tissue. For determining electrolyte leakage (EL), fresh leaf sample was rinsed with distilled water to avoid any surface contamination. Then, 0.5 g fresh leaf disk was sliced into small 15 pieces and put into a test tube with adding 20 ml of distilled water followed by random shaking continuously for 12 h according to [24]. Then, initial conductivity (EC_1) was measured using a conductivity meter (Eutech CON 150, Thermo Scientific Eutech Instrument, Singapore) and followed by heating the sample at 60 °C for 15 min. Subsequently, conductivity (EC_2) was measured and electrolyte leakage was calculated as the ratio between EC_1 and EC_2 that was expressed in percentage as Eq. 2.

$$\text{Electrolyte leakage}\ (\%) = \frac{\text{EC}_1}{\text{EC}_2} \times 100 \quad (2)$$

where, EC_1 is the initial conductivity and EC_2 is the final conductivity of the solution. Similarly, membrane stability index was computed by following the method prescribed by [25]. Where EC_1 is the initial electrical conductivity at 40 °C and EC_2 is the final electrical conductivity at 100 °C.

$$\text{Membrane stability index}(\%) = \left(1 - \frac{EC1}{EC2}\right) \times 100 \quad (3)$$

The leaf's free proline concentration was determined using the method outlined by [26]. Initially, 500 mg of fresh leaf was ground into a paste and mixed with 10 ml of a 3% sulfosalicylic acid solution, then centrifuged at 6,000 rpm for 15 min. About 2 ml sample was combined with 2 ml of acid ninhydrin and 2 ml of glacial acetic acid, heated in a water bath for 30 min. After adding 4 ml of toluene, it was centrifuged at 5,000 rpm for 5 min. The upper layer was separated, and the absorbance was measured at 520 nm using a spectrophotometer to determine the concentration of free proline from standard solutions.

2.5.3 Seed Yield and Yield Attributes

Total seed yield was determined by measuring the weight of individual heads, resulting in the total fresh seed weight. Head diameter was measured using digital slide calipers, and the number of seeds per head was also counted using a seed counter.

2.6 Statistical Analysis

All collected data were effectively analyzed using a three-way analysis of variance (ANOVA) with Statistix version 10 (Analytical Software, 2105 Miller Landing Rd., Tallahassee, FL 32312, USA). Significant treatment effects were identified through the F test and further clarified using Tukey's honest significant difference test ($p < 0.05$). The results were presented in a way that highlights the highest order of factorial combination that demonstrated significance in the ANOVA.

3 Results

3.1 Growth Parameters

The interactive effects between salinity levels and silicon (Si) application, as well as between Si and AMF inoculation, were found to be statistically significant for plant height (Table 2). Across all Si application rates, AMF-inoculated plants exhibited greater plant height compared to non-inoculated counterparts. Stem diameter showed a positive response to increasing Si doses but decreased with higher salinity levels. At 12 dS m^{-1} salinity level, stem diameter increased by 33% with Si_{450} application compared to the control (Si_0) in the absence of AMF. Furthermore, AMF inoculation significantly enhanced stem diameter by 17% and 11% at Si_{150} and Si_{300}, respectively, under the same salinity level (Table 3). Application of silicon significantly improved shoot dry weight, root dry weight, and root volume compared to untreated controls. Although all these parameters declined with increasing salinity stress and it was observed that salinity levels up to 12 dS m^{-1} resulted in a reduction of approximately 45% in shoot biomass and 25%

Table 2 Significance level in the three-way ANOVA of the effect of monosilicic acid dose (MSA), salinity levels (S) and AMF inoculation (AMF) on morpho-physiological traits and seed yield of sunflower

Traits	MSA doses	Salinity levels (S)	AMF inoculation (AMF)	MSA × Salinity	Salinity × AMF	MSA × AMF	MSA × Salinity × AMF
Growth parameters							
Plant height (cm)	ns	*	ns	**	ns	**	ns
Stem diameter (cm)	**	**	**	**	ns	*	*
Shoot dry weight (g plant^{-1})	ns	ns	ns	*	ns	ns	ns
Root dry weight (g plant^{-1})	**	**	**	**	ns	ns	ns
Root volume (cm^3)	**	**	**	**	**	ns	ns
Physiological traits							
Leaf greenness (SPAD value)	**	**	ns	ns	*	**	*
Leaf relative water content (%)	ns	**	*	**	**	**	*
Electrolyte leakage (%)	**	**	**	**	**	ns	**
Cell membrane stability index (%)	**	**	**	**	ns	**	**
Proline concentration (μg g^{-1} fresh weight)	**	ns	**	ns	**	*	*
Yield attributes and yield							
Head weight (g plant^{-1})	*	**	**	ns	ns	ns	ns
Head diameter (cm)	**	ns	ns	**	ns	**	*
Seed number head^{-1}	**	*	**	ns	ns	ns	ns
Seed yield (g head^{-1})	**	*	*	ns	ns	**	*

**, *, and ns indicate $p < 0.01$, $p < 0.05$, and not significant respectively

Table 3 Combined effect of monosilicic acid dose, salinity levels and AMF inoculation on stem diameter of sunflower

Monosilicic acid dose (kg ha^{-1})	AMF inoculation	Stem diameter (cm)			
		0.54 dS m^{-1}	4 dS m^{-1}	8 dS m^{-1}	12 dS m^{-1}
Si_0	–AMF	10.5 ± 2.4cA	9.8 ± 0.5cAB	9.8 ± 1.3cAB	8.3 ± 0.6bB
	+ AMF	11.1 ± 0.3cA	9.8 ± 0.9cAB	9.8 ± 0.4cAB	8.5 ± 0.1bB
Si_{150}	–AMF	11.0 ± 0.8cA	10.1 ± 0.7cAB	9.0 ± 0.6cB	8.6 ± 0.4bB
	+ AMF	11.9 ± 0.3bcA	11.3 ± 0.2bA	11.3 ± 0.3abA	10.1 ± 0.1abA
Si_{300}	–AMF	12.1 ± 0.4bcA	11.8 ± 0.2bcAB	10.8 ± 0.8bAB	10.1 ± 0.6abB
	+ AMF	12.8 ± 0.2bcA	12.5 ± 0.3abA	11.6 ± 0.1abA	11.3 ± 0.3abA
Si_{450}	–AMF	13.2 ± 0.5abA	12.1 ± 0.2bAB	12.1 ± 0.3abAB	11.2 ± 0.6abB
	+ AMF	15.5 ± 0.5aA	15.1 ± 0.3aAB	12.8 ± 0.2abB	12.4 ± 0.8aB

Means followed by same small case letters are statistically similar within a column and means followed by same capital letter are statistically similar within a row based on Tukey's honest significant difference test at $p < 0.05$; data are means of three replications ± standard errors

in root biomass. Conversely, Si application at higher doses led to a 47% and 38% increase in root and shoot dry weight, respectively, under 12 dS m^{-1} salinity level (Figs. 1 and 2). Among the different treatment combinations, the highest root volume was recorded with Si_{450} application and root volume was increased by 37% under Si_{450} compared to the control, whereas it declined by 26% at 12 dS m^{-1} salinity (Fig. 3). Stem diameter exhibited a progressive decline with increasing salinity, yet AMF-inoculated plants consistently maintained greater stem thickness than non-inoculated ones. Notably, plants treated with Si_{450} and AMF showed an 11% increase in stem diameter compared to non-inoculated plants under 12 dS m^{-1} salinity level.

3.2 Physiological Traits

The study revealed that the three-way interaction among monosilicic acid (Si) application rates, salinity levels, and AMF inoculation had a statistically significant effect on several physiological parameters, including chlorophyll content (SPAD value), RWC, EL, MSI, and free proline concentration (Table 2). In the present study, plants treated with both

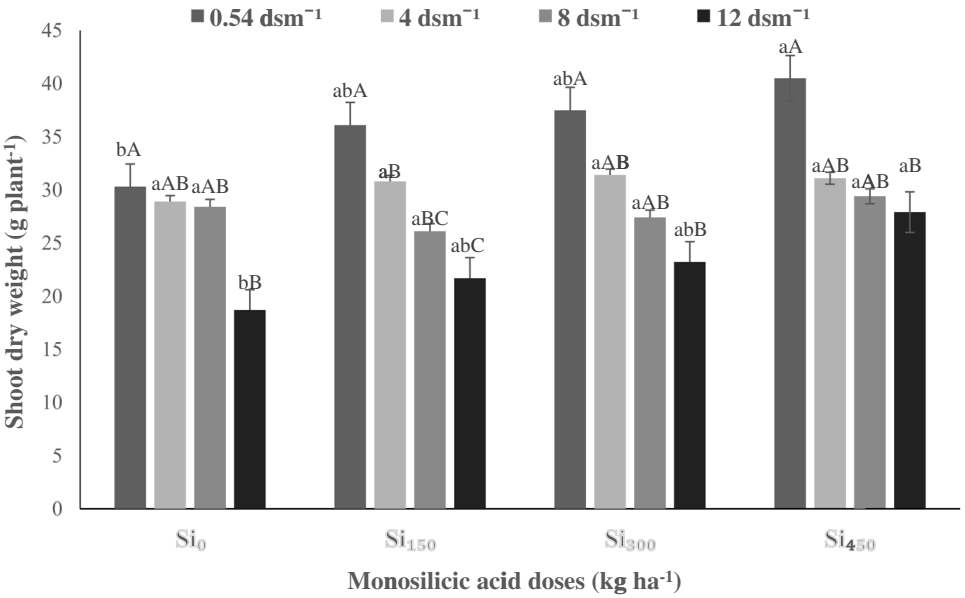

Fig. 1 Interaction between monosilicic acid doses and salinity on shoot dry weight of sunflower. Means followed by the same small case letters are statistically similar within a specific level of salinity under various monosilicic acid doses and means followed by the same upper-case letters are statistically similar within a specific level of monosilicic acid doses under various salinity levels based on Turkey's honest significant difference test at $p < 0.05$; data are means of three replication ± standard errors

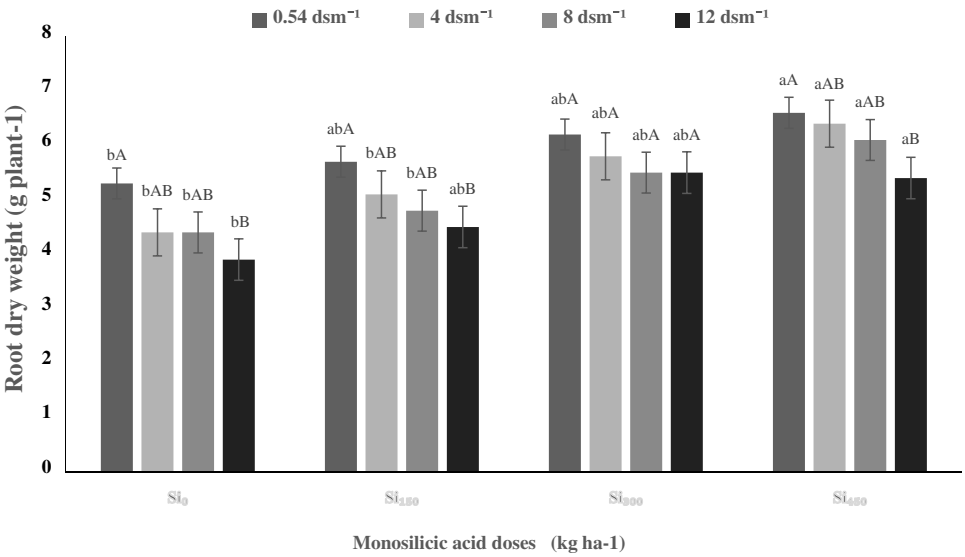

Fig. 2 Interaction between monosilicic acid doses and salinity on root dry weight of sunflower. Means followed by the same small case letters are statistically similar within a specific level of salinity under various monosilicic acid doses and means followed by the same upper-case letters are statistically similar within a specific level of monosilicic acid doses under various salinity levels based on Turkey's honest significant difference test at $p < 0.05$; data are means of three replication ± standard errors

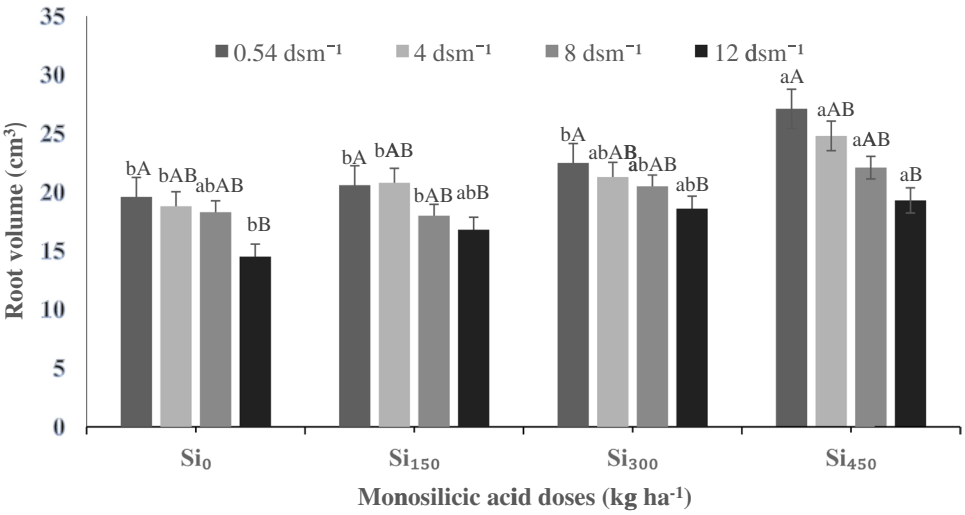

Fig. 3 Interaction between monosilicic acid doses and salinity on root volume of sunflower. Means followed by the same small case letters are statistically similar within a specific level of salinity under various monosilicic acid doses and means followed by the same upper-case letters are statistically similar within a specific level of monosilicic acid doses under various salinity levels based on Turkey's honest significant difference test at $p < 0.05$; data are means of three replication ± standard errors

Table 4 Effect of monosilicic acid dose, salinity levels and AMF inoculation on leaf greenness (SPAD value) and leaf relative water content of sunflower

Monosilicic acid dose (kg ha^{-1})	AMF inoculation	Leaf greenness (SPAD value)				Leaf relative water content (%)			
		0.54 dS m^{-1}	4 dS m^{-1}	8 dS m^{-1}	12 dS m^{-1}	0.54 dS m^{-1}	4 dS m^{-1}	8 dS m^{-1}	12 dS m^{-1}
Si_0	–AMF	37.2 ± 1.7bA	37.2 ± 0.8bA	36.4 ± 0.4aA	34.1 ± 0.8aA	74.1 ± 1.9bA	65.5 ± 4.1cAB	65.1 ± 3.5bAB	54.3 ± 1.9cB
	+ AMF	37.9 ± 1.8bA	37.8 ± 1.9abA	36.3 ± 2.3aA	33.8 ± 0.3aB	78.0 ± 0.2bA	78.5 ± 0.8dAB	70.8 ± 0.4bAB	58.4 ± 8.06bcB
Si_{150}	–AMF	38.5 ± 2.6bA	37.5 ± 2.1abA	37.4 ± 1.3aA	34.1 ± 0.6aB	73.5 ± 4.7bAB	75.4 ± 9.5bA	75.3 ± 9.2abAB	61.4 ± 8.4bcB
	+ AMF	40.1 ± 0.6bA	40.5 ± 0.9abA	38.0 ± 0.8aA	35.4 ± 1.9aB	79.1 ± 2.4bA	78.6 ± 6.9abAB	75.1 ± 0.6abAB	65.2 ± 0.04bcB
Si_{300}	–AMF	40.5 ± 0.4bA	39.9 ± 0.9abA	37.2 ± 0.9aA	36.1 ± 0.4aB	81.2 ± 1.6bA	76.7 ± 0.7abAB	74.6 ± 1.3abAB	65.6 ± 3.7bB
	+ AMF	42.5 ± 0.4abB	40.3 ± 0.9abB	38.3 ± 1.1aB	36.5 ± 1.6aB	87.3 ± 1.3abA	78.7 ± 2.9abAB	76.3 ± 0.01abB	70.4 ± 4.4abB
Si_{450}	–AMF	40.6 ± 0.6bA	38.9 ± 0.6abA	38.9 ± 0.4aA	35.5 ± 1.4aB	86.9 ± 0.4abA	79.4 ± 0.5abAB	78.5 ± 2.7abAB	72.3 ± 1.9abB
	+ AMF	47.9 ± 1.2aA	42.6 ± 0.4aAB	40.6 ± 0.6aB	39.9 ± 2.3aB	92.3 ± 2.8aA	85.3 ± 0.6aAB	80.2 ± 1.05aB	79.6 ± 1.0aB

Means followed by same small case letters are statistically similar within a column and means followed by same capital letter are statistically similar within a row based on Tukey's honest significant difference test at $p < 0.05$; data are means of three replications ± standard errors

Table 5 Three way interaction among monosilicic acid dose, salinity levels and AMF inoculation on electrolyte leakage and cell membrane stability index of sunflower

Monosilicic acid dose (kg ha^{-1})	AMF inoculation	Electrolyte leakage (%)				Cell membrane stability index (%)			
		0.54 dS m^{-1}	4 dS m^{-1}	8 dS m^{-1}	12 dS m^{-1}	0.54 dS m^{-1}	4 dS m^{-1}	8 dS m^{-1}	12 dS m^{-1}
Si_0	–AMF	59.4 ± 0.2aB	60.5 ± 0.2bcAB	59.5 ± 0.1cB	62.6 ± 0.3cA	37.4 ± 2.05cA	34.6 ± 5.6bAB	28.4 ± 1.2bB	12.5 ± 0.6cC
	+ AMF	55.8 ± 0.2bC	58.3 ± 0.4cBC	60.4 ± 0.09cB	70.4 ± 0.6bcA	39.1 ± 0.2bcA	37.5 ± 3.5bAB	30.5 ± 0.8bB	15.7 ± 0.6bcC
Si_{150}	–AMF	59.2 ± 0.2abC	62.0 ± 0.3bcC	67.7 ± 0.06bB	72.9 ± 0.2abA	39.8 ± 2.05bcA	38.9 ± 2.04abAB	32.3 ± 0.9bB	15.1 ± 1.09bcC
	+ AMF	51.9 ± 0.2cC	58.3 ± 0.2cBC	61.8 ± 0.08cB	73.3 ± 0.7abA	42.0 ± 3.6bcA	38.3 ± 3.4bbAB	28.1 ± 3.4bB	16.7 ± 0.3bcC
Si_{300}	–AMF	50.4 ± 0.5cdC	62.4 ± 0.4bB	70.9 ± 0.1aAB	75.4 ± 0.5aA	42.5 ± 0.8abA	41.5 ± 0.09abAB	28.2 ± 2.9bB	19.6 ± 1.9bC
	+ AMF	46.9 ± 0.2dC	55.9 ± 0.1cdB	68.5 ± 0.1abAB	70.5 ± 0.8bcA	44.8 ± 0.6abA	42.1 ± 3.3bbAB	32.4 ± 2.5bB	28.4 ± 3.3abAB
Si_{450}	–AMF	44.6 ± 0.2 dB	68.0 ± 0.3aAB	70.9 ± 0.3aAB	71.9 ± 0.7bA	42.4 ± 2.7bA	39.9 ± 0.2abAB	36.0 ± 0.1abB	19.1 ± 1.1bcC
	+ AMF	44.1 ± 0.3dC	50.1 ± 0.2 dB	59.7 ± 0.1cAB	61.1 ± 0.4cA	48.9 ± 3.8aA	42.8 ± 2.3aB	40.2 ± 0.02aBC	31.9 ± 3.7aC

Means followed by same small case letters are statistically similar within a column and means followed by same capital letter are statistically similar within a row based on Tukey's honest significant difference test at $p < 0.05$; data are means of three replications ± standard errors

Table 6 Effect of monosilicic acid dose, salinity levels and AMF inoculation on proline concentration of sunflower

Monosilicic acid dose (kg ha^{-1})	AMF inoculation	Proline concentration (µg g^{-1} fresh weight)			
		0.54 dS m^{-1}	4 dS m^{-1}	8 dS m^{-1}	12 dS m^{-1}
Si_0	–AMF	450.0 ± 11.5bB	565.0 ± 20.2aAB	570.0 ± 5.7bAB	595.0 ± 2.8bA
	+ AMF	525.0 ± 14.4abB	570.0 ± 25.8aAB	585.0 ± 2.8bAB	725.0 ± 2.8abA
Si_{150}	–AMF	615.0 ± 60.6abA	625.0 ± 20.2aA	648.3 ± 43.3abA	690.0 ± 14.3abA
	+ AMF	675.0 ± 129.9aB	695.0 ± 43.3aB	815.0 ± 42.6aAB	825.0 ± 5.7abA
Si_{300}	–AMF	565.0 ± 11.5abB	575.0 ± 5.7aAB	650.0 ± 69.6abAB	710.0 ± 20.2abA
	+ AMF	575.0 ± 31.7abB	590.0 ± 8.6aAB	600.0 ± 40.4bAB	899.6 ± 34.6abA
Si_{450}	–AMF	580.0 ± 17.3abB	610.0 ± 17.3aB	640.0 ± 40.4abAB	730.3 ± 28.8abA
	+ AMF	650.0 ± 20.2abB	685.0 ± 37.5aAB	880.0 ± 23.09abAB	993.0 ± 20.2aA

Means followed by same small case letters are statistically similar within a column and means followed by same capital letter are statistically similar within a row based on Tukey's honest significant difference test at $p < 0.05$; data are means of three replications ± standard errors

Si and AMF demonstrated superior physiological performance compared to controls, regardless of salinity level. At a salinity level of 12 dS m^{-1}, plants receiving Si at 450 kg ha^{-1} (Si_{450}) soil application combined with AMF inoculation exhibited notable improvements in physiological responses: SPAD value increased by 17%, RWC by 45%, and MSI by 60%, while EL decreased by 15% compared to the control (Tables 4 and 5). A general declining trend in physiological traits was observed with increasing salinity, whereas AMF inoculation mitigated these negative effects. Leaf greenness (SPAD value) remained statistically unchanged between 0 and 8 dS m^{-1} salinity levels (Table 4). However, under 12 dS m^{-1} salinity, AMF inoculation combined with Si_{450} treatment enhanced SPAD values by 12% relative to non-inoculated controls. RWC decreased progressively with rising salinity across all Si levels, but about 10% higher RWC was recorded in plants treated with Si_{450} and AMF at 12 dS m^{-1} over control. Across all Si doses, AMF-inoculated plants consistently maintained higher RWC than non-inoculated ones. EL was significantly affected by the Si treatments, with AMF-inoculated plants exhibiting markedly lower EL values than non-inoculated counterparts. At 12 dS m^{-1} salinity level, Si_{450} application reduced EL by approximately 20% and 15% in AMF-inoculated and non-inoculated plants, respectively. Likewise, MSI was significantly influenced by salinity stress; soil application of Si_{450} enhanced MSI by 70% in AMF-inoculated and by 53% in non-inoculated plants compared to the control (Si_0) at 12 dS m^{-1} (Table 5). Free proline concentration was also significantly affected by the three-way interaction among Si dose, salinity level, and AMF inoculation (Table 6). Proline accumulation increased with rising salinity regardless of AMF inoculation or Si application. At 12 dS m^{-1} salinity, maximum proline accumulation was recorded in plants treated with Si_{450}, representing about 19% and 28% increase over the control for AMF-inoculated and non-inoculated plants, respectively (Table 6). Moreover, AMF-inoculated plants exhibited significantly higher proline accumulation under salinity stress, with 25% and

Table 7 Individual effect of monosilicic acid dose, salinity levels and AMF inoculation on head weight and seed number head^{-1} of sunflower

Monosilicic acid dose (kg ha^{-1})	Head weight (g plant^{-1})	Seed number head^{-1}
Si_0	25.5 ± 1.4b	453.6 ± 14.7b
Si_{150}	26.2 ± 0.7ab	460.3 ± 7.5b
Si_{300}	27.8 ± 2.1ab	506.5 ± 8.2ab
Si_{450}	28.6 ± 0.8a	531.3 ± 11.7a
Salinity levels (dS m^{-1})		
0.54	29.9 ± 1.9a	607.08 ± 14.2a
4	27.8 ± 0.8ab	561.1 ± 5.4b
8	25.3 ± 2.1b	491.5 ± 3.5c
12	21.3 ± 1.1c	472 ± 9.5c
AMF inoculation		
–AMF	23.8 ± 1.3b	363.2 ± 4.5b
+ AMF	30.3 ± 1.8a	512.6 ± 6.2a

Means followed by same small case letters are statistically similar within a column and means followed by same capital letter are statistically similar within a row based on Tukey's honest significant difference test at $p < 0.05$; data are means of three replications ± standard errors

Table 8 Effect of monosilicic acid dose, salinity levels and AMF inoculation on head diameter and seed yield of sunflower

Monosilicic acid dose (kg ha^{-1})	AMF inoculation	Head diameter (cm)				Seed yield (g head^{-1})			
		0.54 dS m^{-1}	4 dS m^{-1}	8 dS m^{-1}	12 dS m^{-1}	0.54 dS m^{-1}	4 dS m^{-1}	8 dS m^{-1}	12 dS m^{-1}
Si_0	–AMF	11 ± 1.4cA	11.5 ± 0.7bA	10.6 ± 0.4bA	10.0 ± 0.5bA	16.7 ± 1.9bA	16.3 ± 3.3bAB	16.5 ± 4.2aAB	11.6 ± 3.2bB
	+ AMF	12.5 ± 0.3abA	11.8 ± 0.3bA	10.9 ± 0.3bB	10.8 ± 0.6bB	18.1 ± 0.4bA	16.4 ± 0.8bAB	17.9 ± 0.8aAB	12.5 ± 1.1bB
Si_{150}	–AMF	11.5 ± 0.3bcA	11.0 ± 0.5bAB	11.4 ± 0.4abAB	10.1 ± 0.4bB	17.2 ± 2.8bA	16.5 ± 1.3bA	15.0 ± 3.4aA	12.8 ± 1.9bA
	+ AMF	12.3 ± 0.3bcA	12.1 ± 0.6bA	12.3 ± 0.7abA	11.0 ± 0.5bA	17.6 ± 0.2bA	16.2 ± 0.9bA	15.5 ± 0.8aA	14.1 ± 0.9abA
Si_{300}	–AMF	12.6 ± 0.3bA	12.1 ± 0.2bA	10.6 ± 0.9bA	11.6 ± 0.3abA	17.4 ± 0.9bA	17.8 ± 2.3abA	16.4 ± 2.3aA	15.3 ± 2.9abA
	+ AMF	13.5 ± 0.3abA	12.0 ± 0.6bA	10.9 ± 0.7bB	11.5 ± 0.7abB	20.3 ± 0.8bA	19.2 ± 0.3abA	20.1 ± 1.8aA	17.5 ± 0.6aA
Si_{450}	–AMF	12.6 ± 0.3bA	12.0 ± 0.5bAB	12.3 ± 0.6abAB	10.5 ± 0.3bB	19.4 ± 1.4bA	20.2 ± 3.1abA	20.1 ± 1.3aA	18.1 ± 0.7abA
	+ AMF	14.3 ± 0.3aA	13.8 ± 0.2aAB	13.5 ± 0.7aAB	12.7 ± 0.7aB	25.9 ± 0.6aA	22.1 ± 0.7aAB	20.9 ± 0.8aB	18.8 ± 0.7aB

Means followed by same small case letters are statistically similar within a column and means followed by same capital letter are statistically similar within a row based on Tukey's honest significant difference test at $p < 0.05$; data are means of three replications ± standard errors

36% greater proline content at Si_{300} and Si_{450}, respectively, compared to non-inoculated plants at 12 dS m^{-1}. Overall, free proline concentration increased with higher Si doses and was consistently higher in AMF-treated plants than in non-inoculated controls under saline conditions.

3.3 Seed Yield and Yield Attributes

The interactive effects among monosilicic acid application rates, salinity levels, and arbuscular mycorrhizal fungi (AMF) inoculation were statistically significant for most yield components and seed yield, excluding head weight and seed number per plant (Table 2). However, the main effects of monosilicic acid doses, salinity stress, and AMF inoculation were individually significant for both head weight and seed number (Table 7). Application of monosilicic acid at a rate of Si_{450} resulted in a 12% and 17% enhancement in head weight and seed number per plant, respectively, relative to the untreated control. AMF inoculation led to a further increase of 23% in head weight and 41% in seed number compared to non-inoculated plants. Salinity stress had a detrimental effect on both parameters, with the highest head weight observed under control conditions and the lowest at the highest salinity level (12 dS m^{-1}) (Table 7). Seed number per plant declined by 27% at 12 dS m^{-1} relative to the control. AMF-inoculated plants consistently outperformed non-inoculated counterparts in seed yield across all silicon treatments. Head diameter was significantly influenced by AMF inoculation, exhibiting a 20% increase under 12 dS m^{-1} salinity when combined with the Si_{450} treatment, compared to the untreated control (Table 8). At the 12 dS m^{-1} salinity level, plants treated with Si_{450} exhibited seed yield increases of 56% and 50% in AMF-inoculated and non-inoculated plants, respectively, relative to those receiving no silicon application (Si_0) (Table 8).

4 Discussion

Soil salinity constitutes a major abiotic stress factor that significantly impairs a range of physiological and biochemical processes, ultimately constraining optimal crop growth and productivity. Elevated concentrations of soluble salts adversely affect all essential plant physiological and metabolic activities, including carbon assimilation, nitrogen metabolism, nutrient acquisition, stomatal conductance, chlorophyll content (leaf greenness), transpiration, and assimilate partitioning [27, 28]. Furthermore, salinity-induced stress accelerates chlorophyll degradation and disrupts the structural and functional integrity of cellular membranes [29], as corroborated by findings in the present study. The data indicated a progressive decline in leaf chlorophyll index (SPAD values) with increasing salinity levels, regardless of treatment application (Table 4). Salinity stress

triggers excessive generation of reactive oxygen species (ROS), which compromise the functional stability of biomolecules including proteins, nucleic acids, membrane lipids, and chlorophyll molecules [30]. ROS, being the byproducts of incomplete oxygen reduction, induce oxidative damage to cellular components under saline conditions [31]. Under salt stress, various reactive oxygen species (ROS) such as superoxide, hydrogen peroxide, hydroxyl radicals, and singlet oxygen are produced in different cellular compartments, disrupting lipid, protein, and nucleic acid metabolism [32, 33]. To mitigate ROS-induced damage, plants activate enzymatic and non-enzymatic antioxidant defense systems. Among these enzymes, superoxide dismutase (SOD) converts superoxide radicals into hydrogen peroxide, thereby protecting cells from oxidative stress. Notably, arbuscular mycorrhizal fungi (AMF)-inoculated plants exhibit higher antioxidant enzyme activities towards lower oxidative damage compared to non-inoculated plants [34, 35].

Numerous studies have established that exogenous application of beneficial elements such as silicon (Si) enhances plant morpho-physiological responses, thereby mitigating the detrimental effects of salt stress, particularly in oilseed crops like sunflower. In the current investigation, root development, physiological parameters, and yield attributes of sunflower exhibited pronounced reductions under escalating salinity stress. However, the combined application of Si and arbuscular mycorrhizal fungi (AMF) markedly alleviated the adverse effects of salinity. Specifically, both leaf greenness and RWC declined significantly with increased salinity across all Si treatments, but AMF inoculation at higher Si concentrations substantially enhanced these parameters compared to sole applications (control) (Table 4). AMF inoculation has been shown to facilitate greater Si uptake relative to non-inoculated plants [36–38], primarily due to the accumulation of silicon in rhizosphere, thereby enhancing silicon bioavailability to host plants [39]. The accumulated Si contributes to the maintenance of cellular water homeostasis by modulating transpiration rates through the formation of a dual-layered cuticle on leaf epidermis, ultimately enhancing photosynthetic efficiency [40, 41]. In addition, Si has been reported to increase stomatal density and aperture size, thereby promoting stomatal conductance and carbon fixation under saline conditions. Silicon also confers protection to photosynthetic pigments against degradation by stabilizing pigment-protein complexes and thylakoid membrane structures, resulting in improved net photosynthetic rates [42, 43]. This enhanced photosynthesis, in turn, supports increased shoot and root biomass accumulation through more efficient carbon assimilation [2].

Furthermore, the presence of silicon (Si) in the rhizosphere enhances the functional efficiency of AMF, contributing to improved root architecture, including increased root length, density, and volume [44, 45]. Silicon application has been shown to improve soil water retention and root absorptive capacity, thereby sustaining plant growth, physiological functioning, and yield under abiotic stress conditions. Consistent with these findings, the current study demonstrated that Si-treated plants exhibited significantly higher RWC compared to the untreated control (Table 4). This improvement may be attributed to Si-induced enhancements in root hydraulic conductance and rhizospheric activity, which collectively facilitate the efficient uptake of water and key mineral nutrients particularly phosphorus (P) under saline conditions. These physiological benefits contribute to improved photosynthetic performance and increased biomass accumulation during stress. Additionally, previous reports have documented that Si fertilization markedly enhances soil hydraulic conductivity and moisture retention capacity, both of which are critical determinants of improved RWC in Si-treated plants [46]. Notably, these studies suggest that the primary mechanism by which Si confers enhanced morpho-physiological resilience and yield stability under suboptimal environmental conditions is through improved soil moisture conservation, rather than direct accumulation of Si within plant tissues.

Moreover, Si accumulation in plants encourage the root activity, reduce lignin synthesis, and enhance the metabolism of phenolic compound in turn up scaling microbial activity in rhizosphere especially AMF effectiveness [47]. Actually, AMF helps plant to reduce salinity stress by absorbing water directly through hyphal network for improving soil physical properties [40]. AMF indirectly reduce the osmotic stress induced by salinity stress through improving soil physical properties like aggregation, infiltration, pore geometry etc. [48, 49]. AMF hyphae enmesh and entangle the soil particles and thus form stable soil aggregates [50, 51]. Moreover, AMF enhance the secretion of GRSP after the hyphal turnover in soil, mucilage, and polysaccharide. These compounds enhance the stability of soil aggregates resulting augment the root biomass, shoot growth and root penetration for absorbing more water in saline soil [52]. The present study depicted that Si_{450} treated plants showed higher root biomass regardless of salinity doses. This result might be due to Si-mediated improvement of root hydraulic conductance and root activity resulting in an efficient absorption of water and mineral, especially P, from soil to maintain a higher photosynthetic rate with more dry matter production under stress condition [53]

Electrolyte leakage (EL) serves as a critical physiological indicator of membrane integrity under salt stress and was observed to increase progressively with elevated salinity levels in the present study. However, the combined application of Si and AMF inoculation significantly reduced EL (Table 5). Enhanced membrane stability and reduced electrolyte efflux were evident in plants receiving AMF inoculation alongside higher Si doses, indicating improved

cellular protection mechanisms. These findings align with previous reports [54–56], which demonstrated lower EL in AMF-inoculated plants compared to non-inoculated controls, attributing this to enhanced membrane stabilization conferred by mycorrhizal symbiosis. AMF facilitates the maintenance of membrane integrity by modulating osmotic balance and mitigating solute leakage from the cytoplasm. The elevated membrane stability index observed in AMF-treated plants suggests the efficacy of AMF in preserving cellular structures under abiotic stress conditions [57]. Salt stress disrupts cellular membranes by altering hydrogen and disulfide bonds in proteins and lipids, leading to membrane destabilization, enhanced ion leakage, and increased lipid peroxidation, typically marked by elevated malondialdehyde (MDA) levels. However, Si application reinforces membrane structure by mitigating oxidative damage, restricting lipid peroxidation, and reducing EL, thereby supporting osmotic regulation and enhancing stress resilience in plants [58].

Osmotic regulation constitutes a critical adaptive mechanism in crop plants for mitigating the adverse impacts of salinity stress by lowering cellular osmotic potential through the accumulation of diverse organic and inorganic osmolytes within the cytoplasm. In the current investigation, proline as a multifunctional osmoprotectant was significantly elevated in plants treated with Si_{450} and inoculated with AMF even under high salinity (12 dS m^{-1}) (Table 8). Proline concentration progressively increased with rising salinity levels and was markedly influenced by the interaction of AMF inoculation and Si supplementation (Table 6). Co-application of Si and AMF resulted in substantial accumulation of compatible solutes such as proline, soluble sugars, and glycine betaine, which enhanced osmotic adjustment and improved RWC. This, in turn, facilitated the biosynthesis and stability of photosynthetic pigments such as chlorophyll and carotenoids for preserving the functional integrity of the photosynthetic apparatus. Proline, an effective organic osmolyte, plays a crucial role in scavenging reactive oxygen species (ROS), protecting cellular biomolecules from oxidative damage, maintaining membrane integrity, and stabilizing enzymes [59–61]. Elevated proline levels are typically associated with increased stress tolerance, with tolerant genotypes accumulating higher concentrations than sensitive ones [62].

Moreover, proline metabolism is tightly linked with ROS detoxification, stress signaling, and reinforcement of the antioxidative defense system [63, 64]. Its direct involvement in ROS quenching, membrane protection, and enzymatic stabilization underpins its pivotal role in salt tolerance [65]. In AMF-colonized plants, proline-mediated osmotic adjustment enhances water uptake, gas exchange, and antioxidant enzyme activities, leading to increased shoot biomass and grain yield, thereby alleviating oxidative damage induced by salt stress [66]. Enhanced biomass production and its effective partitioning towards reproductive structures promote higher grain filling and seed yield. These findings align with previous reports [67, 68] indicating that silicon application in combination with recommended fertilizer dosages improves crop yield and nutrient assimilation. In this study, notable variations in physiological performance and seed yield were observed across Si treatments and AMF inoculation. Thus, the integrated application of Si and AMF represents a viable strategy for enhancing physiological resilience and yield performance of sunflower under saline conditions.

5 Conclusion

The results of the present investigation revealed that shoot and root dry weight was increased by 49% and 38% respectively at Si_{450} compared to control under 12 dSm^{-1} salinity level. Application of Si to plants resulted in a notable improvement in RWC, SPAD value, and MSI by 45%, 17% and 60% respectively, with reducing EL by 15% at salinity level 12 dS m^{-1}. The metabolic fingerprint linked with salinity stress involved accumulation of stress-relieving compounds, mainly proline which was increased by 45% through exogeneous application of Si and AMF. Moreover, plants inoculated with AMF produced higher seed yield than control plants across silicon doses and it has been recorded those plants treated with Si_{450} had promoted seed yield by 56% and 50% in AMF inoculated and non-inoculated plant than Si_0 at 12 dS m^{-1} salinity level. So, integrated application of Si coupled with AMF along with standard fertilizer dose protected salt stressed plants by improving physiological traits, seed yield and ion homeostasis in sunflower.

Acknowledgements The authors express their gratitude to the Bangladesh Bureau of Education Information Statistics (BANBEIS), Ministry of Education, Bangladesh for financial support and Agrotechnology Discipline, Khulna University for logistic support of this research.

Authors Contributions Md. Shariful Islam: Conducted research, data collection, processing and initial draft preparation Md Asadur Rahman: Data collection, processing and initial draft preparation Mst. Sabiha Sultana: Data processing and graph preparation Md. Monirul Islam: Data analysis, review and research investigation Milton Halder: Review and format preparation Debesh Das: Conceptualization, research supervision, critical review and correction.

Funding The authors express their gratitude to the Bangladesh Bureau of Education Information Statistics (BANBEIS), Ministry of Education, Bangladesh for financial support of this research.

Data Availability No datasets were generated or analysed during the current study.

Declarations

Competing interest The authors declare no competing interests.

References

1. Rabbi SMF, Tighe MK, Warren CR, Zhou Y, Denton MD, Barbour MM, Young IM (2021) High water availability in drought tolerant crops is driven by root engineering of the soil microhabitat. Geoderma 383:114738
2. Das D, Basar NU, Ullah H, Salin KR, Datta A (2021) Interactive effect of silicon and mycorrhizal inoculation on growth, yield and water productivity of rice under water-deficit stress. J Plant Nutr 44:2756–2769
3. Roy SD, Das D, Kabir ME (2017) Seed germination and seedling growth of sunflower (*Helianthus annuus L*) under salt stressed conditions. Khulna Univ Stud 14:39–47
4. Alam A, Hariyanto B, Ullah H, Salin KR, Datta A (2021) Effects of silicon on growth, yield and fruit quality of cantaloupe under drought stress. Silicon 13:3153–3162
5. Zargar SM, Mahajan R, Bhat JA, Nazir M, Deshmukh R (2019) Role of silicon in plant stress tolerance: opportunities to achieve a sustainable cropping system. 3 Biotech 9(3):73
6. Tripathi DK, Singh VP, Kumar D, Chauhan DK (2015) Impact of exogenous silicon addition on chromium uptake, growth, mineral elements, oxidative stress, antioxidant capacity, and leaf and root structures in rice seedlings exposed to hexavalent chromium. Acta Physiol Plant 34:279
7. Rizwan M (2015) Silicon-mediated heavy-metal tolerance in durum wheat: Evidences of combined effects at the plant and soil levels. Doctoral thesis, Aix-Marseille Université, France. www.theses.fr/2012AIXM4335/abes. Accessed 20 Mar 2017
8. Chen S, Zhao H, Zou C, Li Y, Chen Y, Wang Z, Jiang Y, Liu A, Zhao P, Wang M (2018) Combined inoculation with multiple arbuscular mycorrhizal fungi improves growth, nutrient uptake and photosynthesis in cucumber seedlings. Front Microbiol 8:2516
9. Ahmed M, Ullah H, Attia A, Tisarum R, Chaum S, Datta A (2011) Interactive effects of *Ascophyllum nodosum* seaweed extract and silicon on growth, fruit yield and quality, and water productivity of tomato under water stress. Silicon 15:2263–2278
10. Raven JA (2023) Cycling silicon—the role of accumulation in plants. New Phytol 158(3):419–430
11. Irfan M, Maqsood MA, Rehman HU, Mahboob W, Sarwar N, Hafeez OBA, Hussain S, Ercisli S, Akhtar M, Aziz T (2023) Silicon nutrition in plants under water-deficit conditions: overview and prospects. Water 15:739
12. Sah SK, Reddy KR, Li J (2022) Silicon enhances plant vegetative growth and soil water retention of soybean (*Glycine max*) plants under water-limiting conditions. Plants 11:1687
13. Li Z, Liu Z, Yue Z, Wang J, Jin L, Xu Z, Jin N, Zhang B, Lyu J, Yu J (2022) Application of exogenous silicon for alleviating photosynthetic inhibition in tomato seedlings under low-calcium stress. Int J Mol Sci 23:13526
14. Thirkell T, Hoysted G, Elliott A, Field K, Daniell T (2020) The use of arbuscular mycorrhizal fungi to improve root function and nutrient-use efficiency. Understanding and improving crop root function, 1st edn. Burleigh Dodds Science Publishing, Cambridge, pp 493–530
15. Ebbisa A (2022) Arbuscular mycorrhizal fungi (AMF) in optimizing nutrient bioavailability and reducing agrochemicals for maintaining sustainable agroecosystems. Arbuscular Mycorrhizal Fungi in Agriculture—New Insights. IntechOpen
16. Mohammadi M, Modarres-Sanavy SAM, Pirdashti H, Zand B, Tahmasebi-Sarvestan Z (2019) Arbuscular mycorrhizae alleviate water deficit stress and improve antioxidant response, more than nitrogen fixing bacteria or chemical fertilizer in the evening primrose. Rhizosphere 9:76–89
17. Pal SC, Hossain MB, Mallick D, Bushra F, Abdullah SR, Dash PK, Das D (2024) Combined use of seaweed extract and arbuscular mycorrhizal fungi for alleviating salt stress in bell pepper (*Capsicum annuum L.*). Sci Hortic 325:112597
18. Zong J, Zhang Z, Huang P, Yang Y (2023) Arbuscular mycorrhizal fungi alleviate salt stress in *Xanthoceras sorbifolium* through improved osmotic tolerance, antioxidant activity, and photosynthesis. Front Microbiol 14:1138771
19. Scavo A, Abbate C, Mauromicale G (2019) Plant allelochemicals: agronomic, nutritional and ecological relevance in the soil system. Plant Soil 442:23–48
20. De Souza TAF, Santos D (2018) Effects of using different host plants and long-term fertilization systems on population sizes of infective arbuscular mycorrhizal fungi. Symbiosis 76:139–149
21. Parça F, Ünay A (2021) A preliminary study on the response of confectionery sunflower (*Helianthus annuus L.*) to arbuscular mycorrhizal fungi (AMF). ANADOLU Ege Tarımsal Araştırma Enstitüsü Dergisi 31(1):1–8
22. Adhikary D, Das D, Ali MY, Ullah H, Datta A (2022) Growth, grain yield, and water productivity of traditional rice landraces from coastal Bangladesh, as affected by salt stress. J Crop Improv. https://doi.org/10.1080/15427528.2022.2048765
23. Das D, Ullah H, Tisarum R, Cha-um S, Datta A (2021) Morpho-physiological responses of tropical rice to potassium and silicon fertilization under water-deficit stress. J Soil Sci Plant Nutr 23:220–237
24. Camejo D, Rodriguez P, Morales MA, Amico JMD, Torrecillas A, Alarcon JJ (2015) High temperature effects on photosynthetic activities of two tomato cultivars with different heat susceptibility. Plant Physiol 162:281–289
25. Hayat S, Hasan SA, Fariduddin Q, Ahmad A (2008) Growth of tomato (*Lycopersicon esculentum*) in response to salicylic acid under water stress. J Plant Interact 3:297–304
26. Bates LS, Waldren RP, Teare ID (1973) Rapid determination of free proline for water-stress studies. Plant Soil 39:205–207
27. Lucini L, Rouphael Y, Cardarelli M, Canguier R, Kumar P, Colla G (2015) The effect of a plant-derived biostimulant on metabolic profiling and crop performance of lettuce grown under saline conditions. Sci Hortic 182:124–133
28. Yin L, Wang S, Li J, Tanaka K, Oka M (2013) Application of silicon improves salt tolerance through ameliorating osmotic and ionic stresses in the seedling of *Sorghum bicolor*. Acta Physiol Plant 35:3099–3107
29. Parida AK, Das AB (2005) Salt tolerance and salinity effects on plants: a review. Ecotoxicol Environ Saf 60(3):324–349
30. Lubitz W, Chrysina M, Cox N (2019) Water oxidation in photosystem II. Photosynth Res 142:105–125
31. Huang S, Leng G, Huang Q, Xie Y, Liu S, Meng E, Li P (2017) The asymmetric impact of global warming on US drought types and distributions in a large ensemble of 97 hydro-climatic simulations. Sci Rep 7(1):5891
32. Muchate NS, Nikalje GC, Rajurkar NS, Suprasanna P, Nikam TD (2016) Plant salt stress: adaptive responses, tolerance mechanism and bioengineering for salt tolerance. Bot Rev 82:371–406
33. Lu YW, Wang GQ, Meng QJ, Zhang WH, Duan BL (2014) Growth and physiological responses to arbuscular mycorrhizal fungi and salt stress in dioecious plant *Populus tomentosa*. Can J For Res 44:1020–1031
34. Das D, Ullah H, Himanshu SK, Tisarum R, Cha-um S, Datta A (2023) Arbuscular mycorrhizal fungi inoculation and phosphorus application improve growth, physiological traits, and grain yield of rice under alternate wetting and drying irrigation. J Plant Physiol 278:153829
35. Mukherjee S, Dash PK, Das D, Das S (2023) Growth, yield and water productivity of tomato as influenced by deficit irrigation water management. Environ Process 10:10
36. Clark RA, Zeto SK (2000) Mineral acquisition by arbuscular mycorrhizal plants. J Plant Nutr 23:867–902

37. Garg N, Kashyap L (2017) Silicon and *Rhizophagus irregularis*: potential candidates for ameliorating negative impacts of arsenate and arsenite stress on growth, nutrient acquisition and productivity in *Cajanus cajan (L.)* Millsp. genotypes. Environ Sci Pollut Res 24:18520–18535
38. Garg N, Bhandari P (2016) Interactive effects of silicon and arbuscular mycorrhiza in modulating ascorbate-glutathione cycle and antioxidant scavenging capacity in differentially salt tolerant *Cicer arietinum L.* genotypes subjected to long-term salinity. Protoplasma 253:1325–1345
39. Hammer EC, Nasr H, Pallon J, Olsson PA, Wallander H (2011) Elemental composition of arbuscular mycorrhizal fungi at high salinity. Mycorrhiza 21:117–135
40. Boling L, Prabhakaran S, Abinaya M (2019) Mechanisms of silicon-mediated amelioration of salt stress in plants. Plants 8:307
41. Ashfaque F, Inam A, Iqbal S, Sahay S (2017) Response of silicon on metal accumulation, photosynthetic inhibition and oxidative stress in chromium-induced mustard *(Brassica juncea L.*). S Afr J Bot 111:153–160
42. Yin Y, Li S, Liao W, Lu Q, Wen X, Lu C (2010) Photosystem II photochemistry, photoinhibition and the xanthophyll cycle in heat stressed rice leaves. Plant Physiol 167:959–966
43. Feng J, Shi Q, Wang X, Wei M, Yang F, Xu H (2010) Silicon supplementation ameliorated the inhibition of photosynthesis and nitrate metabolism by cadmium (Cd) toxicity in *Cucumis sativus L.* Sci Hortic 123(4):521–530
44. Moradtalab N, Hajiboland R, Aliasgharzad N, Hartmann TE, Neumann G (2019) Silicon and the association with an arbuscular-mycorrhizal fungus (*Rhizophagus clarus*) mitigate the adverse effects of drought stress on strawberry. Agronomy 9:41
45. Hajiboland R (2012) Effect of micronutrient deficiencies on plants stress responses. In: Abiotic stress responses in plants. Springer, pp 283–329
46. Hajiboland R, Moradtalab N, Aliasgharzad N, Eshaghi Z, Feizy J (2018) Silicon influences growth and mycorrhizal responsiveness in strawberry plants. Physiol Mol Biol Plants 24:1103–1112
47. Rodrigues FÁ, McNally DJ, Datnoff LE, Jones JB, Labbé C, Benhamou N, Menzies JG, Bélanger RR (2004) Silicon enhances the accumulation of diterpenoid phytoalexins in rice: a potential mechanism for blast resistance. Phytopathology 94:177–183
48. Mardukhi B, Rejali F, Daei G, Ardakani MR, Malakouti MJ, Miransari M (2011) Arbuscular mycorrhizas enhance nutrient uptake in different wheat genotypes at high salinity levels under field and greenhouse conditions. CR Biol 334:564–571
49. Martin SL, Mooney SJ, Dickinson MJ, West HM (2012) The effects of simultaneous root colonisation by three *Glomus* species on soil pore characteristics. Soil Biol Biochem 49:167–173
50. Rillig MC, Mummey DL (2006) Mycorrhizas and soil structure. New Phytol 171:41–53
51. Akter S, Kamruzzaman M, Sarder MP, Amin MS, Joardar JC, Islam MS, Nasrin S, Islam MU, Islam F, Rabbi S, Halder M (2024) Mycorrhizal fungi increase plant nutrient uptake, aggregate stability and microbial biomass in the clay soil. Symbiosis. https://doi.org/10.1007/s13199-024-00994-4
52. Singh PK, Singh M, Tripathi BN (2013) Glomalin: an arbuscular mycorrhizal fungal soil protein. Protoplasma 250:663–668
53. Schaller J, Scherwietes E, Gerber L, Vaidya S, Kaczorek D, Pausch J, Barkusky D, Sommer M, Hoffmann M (2021) Silica fertilization improved wheat performance and increased phosphorus concentrations during drought at the field scale. Sci Rep 11:20852
54. Feng G, Zhang FS, Li XL, Tian CY, Tang C, Rengel Z (2002) Improved tolerance of maize plants to salt stress by arbuscular mycorrhiza is related to higher accumulation of soluble sugars in roots. Mycorrhiza 12:185–190
55. Garg N, Manchanda G (2008) Effect of arbuscular mycorrhizal inoculation of salt-induced nodule senescence in *Cajanus cajan* (pigeon pea). J Plant Growth Regul 27:115–124
56. Kaya C, Ashraf M, Sonmez O, Aydemir S, Tuna AL, Cullu MA (2009) The influence of arbuscular mycorrhizal colonization on key growth parameters and fruit yield of pepper plants grown at high salinity. Sci Hortic 121:1–6
57. Cabo S, Morais MC, Aires A, Carvalho R, Pascual-Seva N, Silva AP, Gonçalves B (2019) Kaolin and seaweed-based extracts can be used as a middle and long-term strategy to mitigate negative effects of climate change in physiological performance of hazelnut tree. J Agron Crop Sci 206:28–42
58. Begum N, Ahanger MA, Zhang L (2020) AMF inoculation and phosphorus supplementation alleviates drought induced growth and photosynthetic decline in *Nicotiana tabacum* by up-regulating antioxidant metabolism and osmolyte accumulation. Environ Exp Bot 176:103926
59. Kaur G, Asthir B (2015) Proline: a key player in plant abiotic stress tolerance. Biol Plant 59:609–619
60. Kumar A, Verma JP, Sharma R (2021) Effect of osmolytes on plant growth and stress tolerance under abiotic stress conditions: a review. J Plant Growth Regul 40:1909–1934
61. Abdelaziz ME, Kim D, Ali S, Fedoroff NV, Al-Babili S (2017) The endophytic fungus *Piriformospora indica* enhances *Arabidopsis thaliana* growth and modulates Na^+/K^+ homeostasis under salt stress conditions. Plant Sci 263:107–115
62. Ahmed M, Ullah H, Attia A, Tisarum R, Chaum S, Datta A (2023) Interactive effects of *Ascophyllum nodosum* seaweed extract and silicon on growth, fruit yield and quality, and water productivity of tomato under water stress. Silicon 15:2263–2278
63. Demidchik V (2014) Mechanism and physiological roles of K^+ efflux from root cells. Plant Physiol 171:696–707
64. Wu HH, Zou YN, Rahman MM, Ni QD, Wu QS (2017) Mycorrhizas alter sucrose and proline metabolism in trifoliate orange exposed to drought stress. Sci Rep 7:42389
65. Evelin H, Devi TS, Gupta S, Kapoor R (2019) Mitigation of salinity stress in plants by arbuscular mycorrhizal symbiosis: current understanding and new challenges. Front Plant Sci 10:470
66. Ellouzi H, Sghayar S, Abdelly C (2017) H_2O_2 seed priming improves tolerance to salinity, drought and their combined effect more than mannitol in *Cakile maritima* when compared to *Eutrema salsugineum*. Plant Physiol 210:38–51
67. Cuong TX, Ullah H, Datta A, Hanh TC (2017) Effects of silicon-based fertilizer on growth, yield and nutrient uptake of rice in tropical zone of Vietnam. Rice Sci 24:283–290
68. Bushra F, Mallick D, Pal SC, Hossain MB, Abdullah SMR, Dash PK, Das D (2025) Silicon and potassium fertilization upgrade resilience in bell pepper against salt stress through boosting root growth and fruit yield. Silicon 17:377–390