Research Article

Mitigation of Salt Stress in Two Wheat Cultivars by Promising PGP Halotolerant *Bacillus* sp. Strain AE-EH1 Isolated from a Marine Environment

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Abstract | Soil salinity is a crucial challenge that restricts plant development and productivity. In this study, we aimed to report a promising marine-derived plant growth promoting (PGP) bacteria that can empower wheat plants to survive upon salt stress. Thirty-one bacterial isolates derived from marine environments were isolated and assessed for PGP activities. Among these tested isolates, a strain coded as AE-EH1 showed promising PGP activities. Based on the phenotypic characterization, using 16S rRNA gene sequencing, phylogenetic, and biochemical analyses, the selected isolate was identified as *Bacillus* sp. strain AE-EH1 and assigned an accession no. of OR144427. The target strain AE-EH1 could produce indole acetic acid, ammonia, and HCN, furthermore, it could fix atmospheric nitrogen and solubilize phosphate. Meanwhile, the AE-EH1 was characterized as a halotolerant bacterium with a tolerance limit of up to 15 % NaCl with optimum growth at 3 % NaCl. Interestingly, AE-EH1 showed a high *in vitro* antagonistic effect against 6 common plant pathogenic fungal species, including *Botrytis fabae*, *B. cinerea*, *Fusarium oxysporum*, *Macrophomina phaseolina*, *Rhizoctonia solani*, and *Sclerotinia sclerotiorum*. Inoculating, AE-EH1 into wheat *cvs*. Sakha 95 and Masr 3 under salt stress markedly improved the salt tolerance of these wheat cultivars. Moreover, fresh and dry weights of wheat cultivars had improved compared to non-treated plants as well as chlorophyll *a*, *b*, and carotenoids. Total carbohydrates, proteins, and lipids were increased in both Sakha 95 and Masr 3 cultivars as an influence of bacterial strain inoculation. Antioxidant peroxidase, catalase, and proline contents were accumulated in both wheat varieties. Our study provides a promising bacterial strain that can alleviate salt stress and enhance the growth and productivity of wheat under stress and normal conditions.

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Introduction

Soil salinity is an exacerbated burden worldwide concomitant with decreasing soil fertility, low crop yield, and subsequently exhaustion of the economy (Kumawat *et al.*, 2023). About one fifth of the cultivated land is suffering from salinization (Omar *et al.*, 2024). Salinity in soil is owing to

different predisposing factors, including increased water evaporation with rainfall paucity, desertification, inadequate drainage, using salty water due to marginal irrigation, and leakage of sea water into low level lands (Kumawat *et al*., 2023). Productivity and sustainability of crop plants such as wheat and rice are hampered in salty soil due to perturbation in the physiological, morphological, biochemical, and genetic features of the plant (Patwa *et al*., 2024; Alghabari and Shah, 2025). Oxidative damage is one of the major implications of salt stress on plants. Reactive oxygen species (ROS) leads to DNA fragmentation, perturb cell permeability, degrade macromolecules, decrease absorption of potassium and calcium, and impedes enzymatic action (El-Shazoly *et al*., 2024). Furthermore, soil microbiome is altered as a result of salinization (Li *et al*., 2024). Plant growth promoting bacteria (PGPB) inhabiting soil are negatively retarded upon salt stress (Liu *et al*., 2025). The adhering ability of *Azospirillum brasilense* with wheat root has been undermined in high salinity soil (Sahab *et al*., 2021). Based on the previous information, it is crucial to ameliorate crop resistance upon salt stress.

Numerous strategies have been adopted to mitigate salt stress such as improving drainage system and channelizing the farmers to using salt-resistant microbial strains (Chen *et al*., 2024; Valencia-Marin *et al*., 2025). Currently, PGPB are extensively addressed as a sustainable way to increasing crop durability in order to withstand salt stress and promoting soil fertility via chelating sodium ion and increasing gases diffusion cross plant stomata, which in turn improve photosynthetic process and intracellular accumulation of osmolytes (Sánchez *et al*., 2023; Dolu *et al*., 2025). Inoculating PGPB with plant seeds improves plant growth, photosynthetic activities, and crop yield (Dadaşoğlu, 2024). PGPB are multifunctional that employed diverse mechanisms to enhance crop growth and productivity. They can facilitate nutrient uptake *via* different methods such as phosphorus solubilisation, nitrogen fixation, and iron acquisition, as well as production of plant growth modulators, and production of bioactive molecules and lytic enzymes that protect plant against phytopathogens (Timofeeva *et al*., 2023; Wei *et al*., 2024). The rhizosphere associated PGPB *Arthrobacter protophormiae* and *Dietzia natronolimnaea* have improved wheat crop under salt stress *via* up-regulating the content of indole acetic acid (IAA) in wheat crop and restrain the level of abscisic acid (ABA) and 1-aminocyclopropane-1-carboxylate (ACC) (Barnawal *et al*., 2017). Recently, Ji *et al*., (2022) declared that inoculating wheat seeds with the PGPB *Bacillus subtilis* HG-15 and *B. velezensis* JC-K3 has improved wheat yield under low salt stress. Bacteria naturally inhabit saline environment and possess sophisticated genetic machinery and remarkable phenotypic characteristics for adaptation in such cruel conditions. Similar to soil PGPB, halo-bacteria possess PGP traits which can alleviate crop salt stress (Gupta *et al*., 2021; Kumawat *et al*., 2021). Five halotolerant and halophilic bacteria have been shown to produce PGP and enhancing the wheat growth under 200 mM salt stress (Orhan, 2021).

Wheat crop (*Triticum aestivum* L.) is the most nutrient cereal in the world and specifically in Egypt. Around 9 million tons of wheat are produced annually in Egypt representing the total wheat cropping area; however, these amounts are not adequate for more than 100 million populations. Therefore, Egypt is considered as the top importer of the wheat worldwide (Gebeltová *et al*., 2023). As mentioned earlier, salinity is a crucial problem that hampers wheat growth. Improving the ability of wheat to tolerate salt stress enables widening in culturing wheat in wide range of lands that may fill the gap between wheat production and consumption. The objective of this study was to use PGPB isolated from marine environments to alleviate salt stress and enhance wheat growth under abiotic salt stress conditions.

Materials and Methods

Samples collection, chemicals, media and isolation process

Sample collection: Ten samples of marine sediments and sea water were collected from distinct regions in the Mediterranean Sea and the Red Sea, Egypt. These samples were collected in sterile screw cap bottles, clearly labeled, transported immediately under aseptic conditions to the microbiology laboratory, and stored at 4 ˚C for further analysis.

Media and chemicals: Sea water agar (SWA) medium was used to isolate the bacterial isolates that consisted of (g/ L): peptone 5.0, beef extract 3.0, and agar 20. The medium ingredients were dissolved in 1000 ml sea water. The pH was adjusted to 7, then autoclaved at 121 ˚C for 20 min (Binaeian *et al*., 2013). The chemicals, reagents, and solvents used in this study

were of analytical grades with high purity ≥ 98 %.

Isolation process: Each sediment sample was cultured by a spread plate method using SWA medium. Briefly, 1 ml of each soil sample was suspended in 10 ml autoclaved saline solution (0.08 % NaCl) with vigorous vortex mixing, and then serial dilution was made up to 10^{-7}. About 100 µL of each dilution was individually spread over SWA plates using a sterile glass spreader and then incubated at 37 ˚C for 72 h (Singh, 2024). After incubation, all different colonies that developed on the plates were selected and subjected to purification. The purified isolates were cultured on sea water agar slants and preserved at 4 ˚C for further investigation.

Determination of the plant growth promoting (PGP) traits of the bacterial isolates

To determine the PGP-strains, all bacterial isolates were examined for their ability to perform atmospheric nitrogen (N_2) fixation, phosphate solubilization, and produce indole acetic acid (IAA), ammonia (NH_4), and hydrogen cyanide (HCN).

Nitrogen fixation and phosphate solubilization: Atmospheric N_2 fixation capability of all the isolated bacteria was assessed using nitrogen-free medium (NFM) (Khedher *et al*., 2021). All bacterial isolates were individually inoculated on NFM and incubated for 7 d at 37 ˚C. The isolates with capability to grow on NFM were defined as nitrogen fixing bacteria. For phosphate solubilization assay, all the isolated bacteria were grown by streaking on Petri plates of Pikovskaya's modified medium (Surange *et al*., 1997), and incubated at 35 ˚C for 7 d. After incubation, presence of clear zones around the bacterial growth indicates positive phosphate solubilization activity.

Production of IAA, ammonia (NH_4) and hydrogen cyanide (HCN): A colorimetric method was used to determine IAA production (Petrillo *et al*., 2021). Briefly, all the isolated bacteria were cultured on tryptone yeast extract broth and incubated at 35 ˚C for 4 d in orbital shaker at 150 rpm followed by centrifugation 24000 g for 15 min. Then, 1 ml of the supernatant was mixed with 2 ml of Salkowski's reagent (2 % 0.5M $FeCl_3$ in 35 % $HClO_4$ solution), and the mixture was left in darkness for at least 30 min. Development of pink color indicates a positive result (Damodaran *et al*., 2013). The optical density was measured at 530 nm using a spectrophotometer (JENWAY, 7315, UK) to quantify the produced IAA. To detect (NH_4) production, the isolated bacteria were inoculated in peptone water, incubated at 35 ˚C for 5 d in a rotary shaker at 150 rpm. After incubation, 0.2 ml of each culture was mixed with 1 ml Nessler's reagent, where development of brown to yellow color indicates a positive result. The optical density (OD) at 450 nm was measured using a spectrophotometer (JENWAY, 7315, UK) to quantify the produced (NH_4) (Marques *et al*., 2010). The ability of the bacterial isolates to produce HCN was detected using the previous method described by Lorck (1948).

Identification of the potent PGP-strain

To identify the potent PGP-strain, the total DNA was extracted using bacterial genomic extraction kit (Takara, Japan), according to the manufacturer's instructions. The genomic DNA was used as template for polymerase chain reaction (PCR) amplification of 16S rRNA gene using forward and reverse universal primers (27F: AGAGTTTGATCCTGGCTCAG, 1492R: AAGGAGGTGATCCAGCC). The amplification products were purified and sequenced. The obtained sequence was deposited to GenBank and aligned with closely related species sequences obtained from the NCBI database using BLAST (https://blast.ncbi.nlm.nih.gov/Blast.cgi). A phylogenetic tree was constructed using MEGA X software version 11 (Tamura *et al*., 2021) with a neighbor-joining algorithm (Saitou and Nei, 1987).

For scanning electron microscopy (SEM) observation, fresh broth culture of selected bacterium was centrifuged, the pellets were washed twice with saline solution, fixed with glutaraldehyde (2.5 %, v/v), washed with water, and then post-fixed in osmium tetroxide (1 %, w/v) for 1 h. The sample was washed twice with water, dehydrated in ascending ethanol concentrations, and finally examined using SEM (15-20 KV in JEOL JSM 5400 LV, SEM, Japan), at the electron microscope unit of Assiut University, Assiut, Egypt.

Tolerance of potent PGP-strain towards salt stress

To determine the salt tolerance, the selected bacterial strain was inoculated in nutrient broth (NB) medium supplemented with different NaCl concentrations (0, 3, 6, 9, 12, 15, 18, and 19 %), and incubated for 5 d at 35 ºC in a rotary shaker at 150 rpm (Wang *et al*., 2021). The growth of the strain was monitored by measuring the OD at 600 nm within 12 h intervals.

Antagonistic activity of the selected strain against some plant pathogenic fungi

A dual culture technique (Oldenburg *et al*., 1996) was used to investigate the *in vitro* antagonistic impact of the selected bacterial strain against six plant pathogenic fungi, including *Botrytis fabae*, *Botrytis cinerea*, *Fusarium oxysporum*, *Macrophomina phaseolina*, *Rhizoctonia solani* and *Sclerotinia sclerotiorum*. These fungi were obtained from Assiut University, Moubasher Mycological Centre Culture Collection (AUMMC). The target bacterial strain was freshly cultured on nutrient agar (NA) medium at 28 ˚C for 24 h while the fungal strains were cultured on potato dextrose agar (PDA) at 28 ˚C for 5 d. The antagonistic efficacy assay was performed on NA medium and the antagonistic area was estimated by measuring the inhibition zone diameters (mm) formed between the growths of the tested microorganisms using a calibrated ruler.

Preparation of cultivation soil, wheat seeds and bacterial inoculum

The experiment of cultivation in the greenhouse was performed in plastic pots (30 cm in diameter) filled with about 4 Kg of normal clay soil collected from the agricultural area of the campus of Faculty of Science, Al-Azhar University, Assiut, Egypt. The two wheat cultivars (*Triticum aestivum* L.) used in this study with common names *cvs.* Sakha 95 and Masr 3 were obtained from the Agricultural Research Center, Sohag, Egypt. The wheat seeds were surface sterilized by soaking in sodium hypochlorite (3 %) for 5 min. followed by 5 times washing with sterilized dist. water. The sterilized seeds were soaked in the bacterial broth (10^9 CFU/ mL) for 4 h and then dried for 1–2 h at room temperature (Wang *et al*., 2021). To prepare the bacterial inoculum, the PGP-strain was grown in NB medium for 48 h at 35 ºC in a rotary shaker at 150 rpm. All the growing experiments were conducted inside a greenhouse under normal conditions.

Experimental design and plant cultivation

The experiments were carried out at the greenhouse and laboratories of Botany and Microbiology Department, Faculty of Science, Al-Azhar University, Assiut, Egypt. The cultivation experiments were designed to use 4 different concentrations of salt stress (*i.e.*, 0, 50, 100 and 150 mM of NaCl) on wheat plants individually (*cvs*. Sakha 95 and Masr 3). Six pots were used for each salt concentration in each wheat cultivar, 3 of them used for treated plants with selected PGP-strain and the other 3 were used as untreated control pots (plants without inoculation of PGP-strain) with a total of 24 pots for each wheat cultivar. All pots were seeded with 10 grains in each pot (1 cm depth), irrigated with tap water (equal volume for all pots) every 6 d until the fourth leaf appearance, and the pots were irrigated once weekly (1.5 L) with salty water using NaCl. The selected PGP-strain was inoculated ito the treated pots by adding 5 ml of fresh NB culture (1×10^9 cfu/ml) before irrigation with salty water. Meanwhile, the bacteria-free nutrient broth was added (5 ml) to the untreated pots as controls. Pots were arranged in completely randomized design with three replications for each treatment.

Plant harvest and biochemical analysis

The plants of both wheat *cv*s. Sakha 95 and Masr 3 were harvested after 80 d of seeding the grains by cutting the shoot system for each plant individually using a scissor. The separated shoot systems were cut into small fragments and weight to estimate their fresh weight (g/ pot) and then kept at -20 ˚C for further experiments. To record the dry weight (g/ pot), the plant fragments were oven-dried at 70 ˚C for 72 h and then weight.

Determination of photosynthetic pigments: The contents of plant photosynthetic pigments (chlorophyll *a*, *b* and carotenoids) were detected using the spectrophotometric method described by Lichtenthaler (1987). To extract the pigments, 0.5 g of a fresh shoot system was suspended in 5 ml ethyl alcohol (95 %) and heated at 60-70 ˚C in a water bath until the shoot color disappeared. The total volume was completed to 10 ml with 95 % ethyl alcohol and then the absorbance was measured by a spectrophotometer (JENWAY, 7315, UK) at wavelengths of 663, 644, and 452 nm for estimation of chlorophyll a, b and carotenoids, respectively (Lichtenthaler, 1987).

Determination of total carbohydrates, proteins and lipid peroxidation: The total contents of carbohydrates in both *cvs*. Sakha 95 and Masr 3 were determined using the method described by Hewitt (1958). A 0.5 g of dry shoot tissue was mixed with 10 ml of HCl (4 N) in a test tube and heated in a boiling water bath for 1 h. Finally, this solution was cooled, filtered in sterilized vials, and kept in refrigerator until use. Sample extract (0.1 ml) and 4.5 ml anthrone-sulphuric acid reagent were thoroughly mixed and boiled in a water bath for 7 min., and the absorbance

of the developed blue green color was determined at 620 nm (Hewitt, 1958).

For determination of total protein, an alkaline solution of fresh shoot tissue was prepared by adding 10 ml of NaOH (1N) to 0.5 g of fresh tissue in a test tube and boiled in a water bath for 1 h. After boiling, the mixture was filtered in sterilized tube and kept at -20 ˚C. Afterward, 5 ml of the alkaline reagent solution were added to 0.1 ml of the plant extract, mixed, and allowed to stand at room temperature for 10 min. Then, 0.5 ml of diluted Folin Ciocalteau's reagent (1:2 v/v) was added and mixed rapidly. After 30 min., the absorbance of the samples against an appropriate blank was read at 600 nm (Lowery *et al.*, 1951). Lipid peroxidation was determined by measuring malondialdehyde (MDA) formation using the thiobarbituric acid reaction as described by Hodges *et al.* (1999), with slight modifications (Singh and Jha, 2017).

Determination of peroxidase, catalase and proline: Peroxidase activity was determined according to Maehly and Chance (1954). The previously heated enzyme extract (0.5 ml) in water bath (45 ˚C) for 5 min. was added to 3 ml of reaction solution. The reaction solution was prepared as follows (10 mM KH_2PO_4/K_2HPO_4, pH 7.0, 10 mM H_2O_2, and 20 mM guaiacol or catechol). The formation of tetraguaiacol was estimated using a spectrophotometer at 470 nm (Maehly and Chance, 1954). Catalase assay was determined by monitoring the reduction in the absorbance of H_2O_2 at 240 nm. For catalase determination, 100 µl of an enzyme extract were added to 50 mM phosphate buffer (pH 7.8), 0.1 mM EDTA, and 12.5 mM H_2O_2 with a total volume of 3 ml. The activity was calculated based on an extinction coefficient of 0.04 mM/l at 240 nm (Singh and Jha, 2017). Proline content was determined according to Bates *et al.* (1973) using ninhydrin and glacial acetic acid. The absorbance was measured at 520 nm and the standard curve was conducted for proline estimation. The proline concentrations were calculated and expressed as mg/ g dry weight (DW) (Bates *et al.*, 1973).

Statistical analysis

The standard deviation (±SD) is shown by error bars, and data are the means of three comparable replicates. The kinetic analysis was performed using OriginPro 2024. Statistical analysis was conducted on CoStat, Software for windows. Using Compare Means (one-way ANOVA), LSD, and Dunnett's T3 multiple comparison test, the differences between groups and treatments were examined. A *p*-value of less than 0.05 was considered significant.

Results

Isolation of bacterial strains

Thirty-one bacterial isolates were obtained in this study from 10 samples collected from different five regions along the Mediterranean and the Red Sea coast in Egypt. Nineteen isolates (61.2 %) were from water samples, while the remaining isolates (12 isolates, 38.7 %) were from the sediment samples. Concerning Gram reaction, twelve isolates were Gram (+) while 19 were Gram (-).

Detection of PGP-bacteria

All isolates were investigated for 5 PGP activities including IAA production, N_2 fixation, NH_4 production and HCN production, and phosphate solubilization. Table 1 shows the results of testing all strains for PGP activities. For IAA production, all investigated strains were able to produce IAA in different values that ranged from high levels (295.9± 3.0, 279.9± 3.8, 248.2± 3.5, 246.9± 3.2, 226.2± 3.9, and 220.2± 3.8 mg/l as detected in isolates no. 11, 2, 10, 3, 14, and 29, respectively), moderate levels as observed in isolates no. 6, 9, 28, and 13, and low levels as recorded in isolates no. 31, 24, 22, 21, and 17. Concerning N_2 fixation, only 4 isolates (no. 2, 5, 29, and 30) were able to fix atmospheric N_2, as indicated from their ability to grow on NFM.

As shown in Table 1, all bacterial isolates were able to produce NH_4, where the highest production values were recorded in isolates no. 28, 17, 16, 18, 3, 7, and 27, ranging from 646.7±5.3 to 513.3±4.8 mg/ l. According to the results demonstrated in Table 1, approximately 74 % of the bacterial isolates were able to produce HCN. Among the studied isolates, the highest HCN production was detected in isolates no. 27 and 29 followed by isolates no. 2, 4, 13, and 23. For phosphate solubilization, only 4 bacterial isolates were able to solubilize phosphate (no. 11, 16, 26, and 31).

According to the results obtained during the assessment of PGP traits for all the isolated bacteria, isolate no. 29 only has shown promising results and was selected for further studies to test its effect on alleviating salt stress in wheat cultivars.

Table 1: *Plant growth promoting traits, Gram staining and source of isolation of the bacterial isolates.*

[a]Plant growth promotion					Gram stain	Isolation source	Isolates no.
Phosphate solubilization	**HCN production**	**Ammonia production (mg/ L)**	**Nitrogen fixation**	**IAA (mg/ L)**			
- ve	+	146.7± 3.5	- ve	147.6± 3.5	+	W	1
- ve	++	280.0± 4.3	+ ve	279.9± 3.8	-	W	2
- ve	+	513.3± 4.5	- ve	246.9± 3.2	+	W	3
- ve	++	313.3±3.7	- ve	163.2±2.1	+	S	4
- ve	- ve	380.0±4.1	+ ve	166.9±2.0	-	S	5
- ve	+	413.3±4.2	- ve	213.6±1.9	-	S	6
- ve	+	513.3±4.9	- ve	171.2±3.2	+	S	7
- ve	+	380.0±3.6	- ve	113.6±2.4	+	S	8
- ve	+	446.7±4.8	- ve	206.2±2.3	-	W	9
- ve	+	480.0±5.0	- ve	248.2±3.5	+	W	10
+ ve	-ve	346.7±4.0	- ve	295.9±3.0	+	S	11
- ve	+	413.3±4.3	- ve	157.9±3.7	-	W	12
- ve	++	280.0±2.9	- ve	177.2±2.8	-	W	13
- ve	- ve	413.3±4.2	- ve	226.2±3.9	-	W	14
- ve	+	480.0±4.7	- ve	126.9±2.7	+	W	15
+ ve	- ve	580.0±5.6	- ve	150.9±3.9	-	W	16
- ve	+	613.3±5.8	- ve	79.6±1.8	-	W	17
- ve	+	546.7±5.1	- ve	135.9±2.0	+	W	18
- ve	+	180.0±3.9	- ve	82.6±1.4	-	W	19
- ve	+	380.0±3.4	- ve	88.2±2.0	-	W	20
- ve	+	380.0±3.8	- ve	79.9±2.1	-	S	21
- ve	-ve	246.7±3.6	- ve	85.5±2.5	+	S	22
- ve	++	113.3±2.1	- ve	147.6±2.9	+	S	23
- ve	- ve	280.0±3.1	- ve	73.4±2.0	-	S	24
- ve	+	313.3±3.6	- ve	137.0±2.3	+	S	25
+ ve	- ve	446.7±4.5	- ve	150.2±1.8	-	W	26
- ve	+++	513.3±4.8	- ve	140.9±1.8	-	W	27
- ve	+	646.7±5.3	- ve	185.6±2.4	-	W	28
- ve	+++	313.3±4.0	+ ve	220.2±3.8	-	W	29
- ve	+	413.3±4.3	+ ve	140.6±3.4	-	S	30
+ ve	- ve	480.0±4.8	- ve	86.2±2.6	-	W	31

Where;[a]All results were conducted in three independent replicates, *+ ve indicates positive results, - ve indicates negative results, + indicates low production, ++ indicates moderate production, and +++ indicates high production. (W) refer to water, (S) refer to sediment, (HCN) hydrogen cyanide, (IAA) indole acetic acid, (±SD) the standard deviation of three independent replicates.*

Identification of the selected PGP-bacterium

The potent PGP isolate no. 29 was identified using 16S rRNA gene sequencing. The obtained gene sequence (1075 bp) was deposited in GenBank with accession number OR144427, and related sequences were obtained by BLAST. The related sequences with high similarity were analyzed by MEGA software to draw the phylogenetic tree. The obtained tree (Figure 1A) showed that the bacterial strain was closely related to *Bacillus* sp. strain *licheniformis* (similarity 99.91 %) and *Bacillus* sp. strain B11 (similarity 99.81 %). SEM showed the morphological cell shape (bacilli) and the size of this bacterial strain was 1.4 µm × 0.7 µm as shown in Figure 1B. Based on morphology, biochemical assays, and 16S rRNA gene sequencing, this bacterial strain was identified as *Bacillus* sp. strain AE-EH1.

Salt tolerance of Bacillus sp. strain AE-EH1

Salt tolerance of the strain AE-EH1 towards high

salt concentrations was investigated (Figure 2). Strain AE-EH1 demonostrated high salt tolerance, where the growth was not affected by salt concentration increasing up to 6 % NaCl, which was almost equal to the growth of NaCl-free medium (0 %). Despite its ability to thrive, tolerate, and grow in high NaCl concentrations (up to 15 % NaCl), the highest growth of the strain AE-EH1 was detected at 3 % of NaCl (OD 1.82), compared to OD of 1.75 in NaCl-free medium.

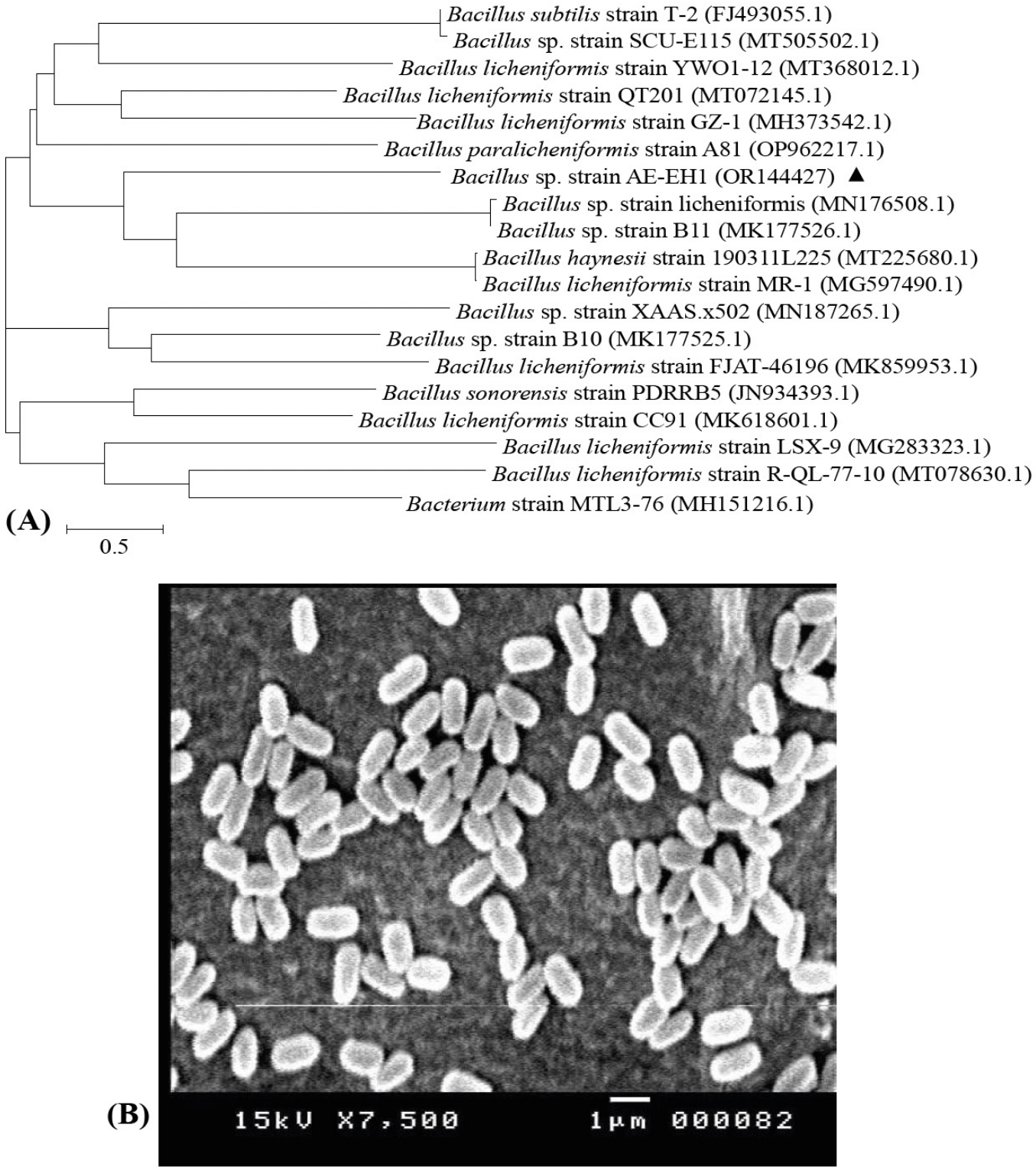

Figure 1: *(A) Neighbor-joining (NJ) phylogenetic tree based on 16S-rDNA sequences of selected bacterial strain aligned with closely related bacterial strains accessed from the GenBank. Bootstrap values included 1000 replicates for the neighbor-joining method using software MEGA-5 (Molecular Evolutionary Genetics Analysis, version 5.2), triangle represent our strain AE-EH1, (B) Scanning electron microscope investigation showing the bacillus cell shape and size (1.4 µm × 0.7 µm).*

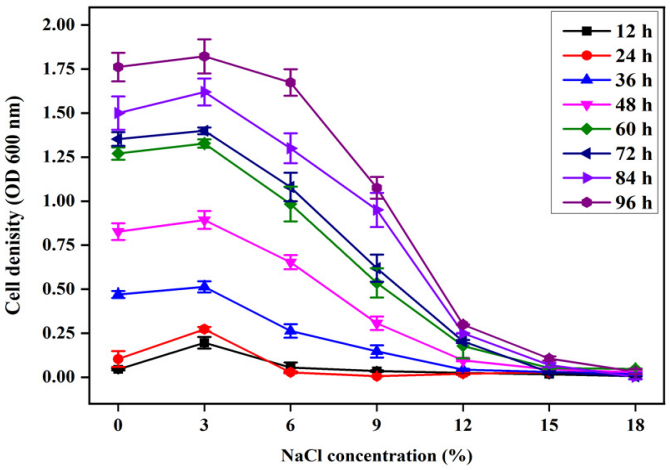

Figure 2: *NaCl tolerance and halophilicity of Bacillus sp. strain AE-EH1at different incubation time intervals. Error bars indicate the standard deviation (±SD) for three independent replicates.*

Antagonistic effect of Bacillus sp. strain AE-EH1 against several fungal pathogens

The target bacterial strain AE-EH1 was assessed for its *in vitro* antifungal activity against 6 of the most common plant pathogenic fungal strains. Interestingly, the AE-EH1 strain exhibited promising activities against all the tested fungi that ranged from high, moderate to weak activities as illustrated in Figure 3. The highest antifungal activity was observed against *B. cinerea* followed by *B. fabae* and *S. sclerotiorum* with inhibition zone's diameters of 18, 15, and 12 mm, respectively, whereas the moderate antagonistic effect was observed against *F. oxysporum* and *M. phaseolina* with inhibition zones of 10 and 8 mm. The weakest antifungal activity was recorded with *R. solani* (5 mm), which exhibited less sensitivity to the tested bacterial strain AE-EH1.

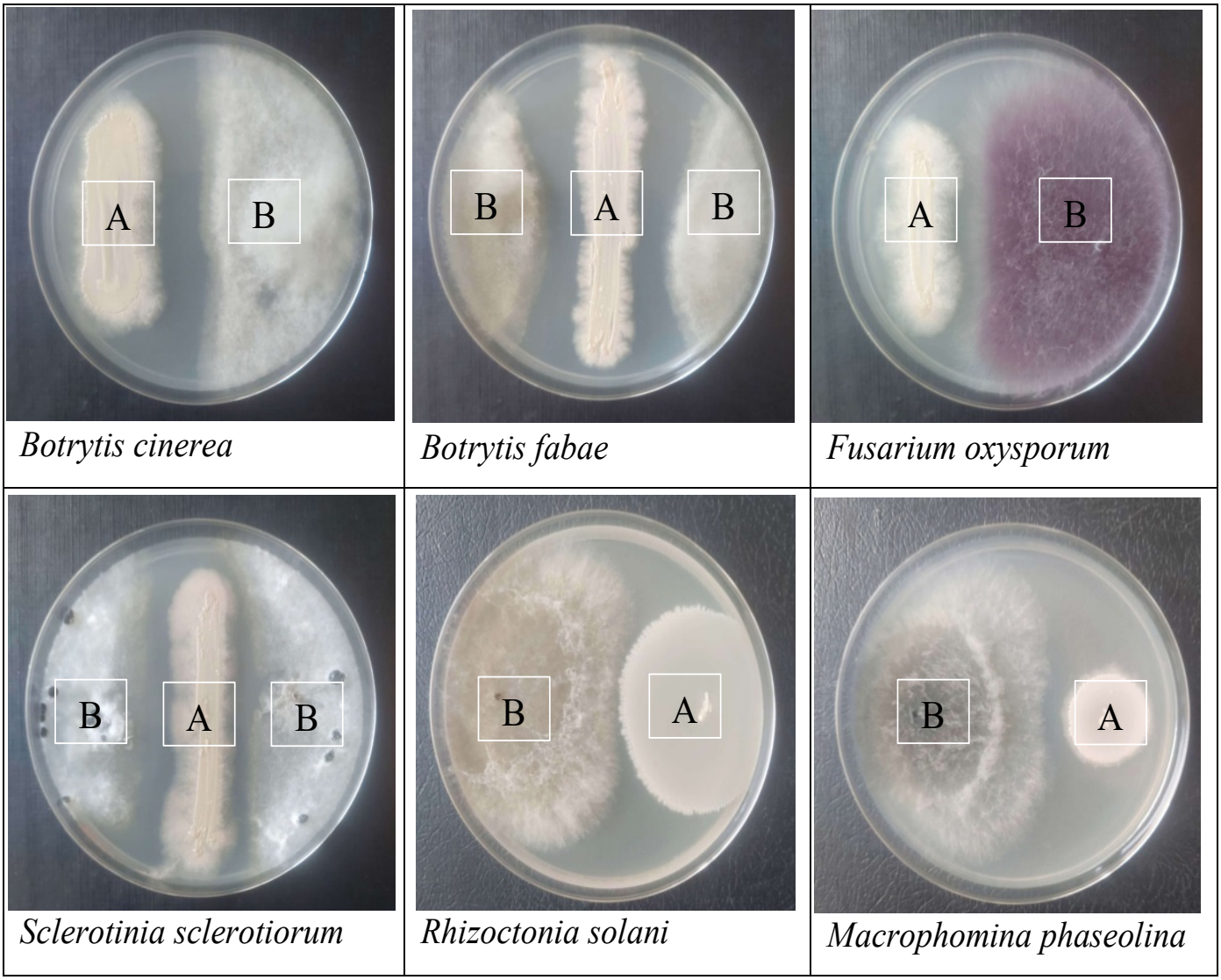

Figure 3: *In vitro antagonistic activity of Bacillus sp. strain AE-EH1 against 6 different plant-pathogenic fungi using dual culture technique. The letter A represents the growth of Bacillus sp. strain AE-EH1, while B represents fungal growth.*

Effect of salt-tolerant Bacillus sp. strain AE-EH1 on growth of wheat plants under salt stress in the greenhouse

At all, the *Bacillus* sp. strain AE-EH1 showed promising *in vivo* growth promoting results for both Masr 3 and Sakha 95 wheat cultivars, and this was implicated from the improvements of the measured growth parameters of the treated over the non-treated plants. The treated plants displayed improvements in the plant length, green color, and total health of wheat plants compared to the non-treated ones (Figure 4). The treated plant length of Masr 3 improved with ~20 % compared to non-treated plants in low saline concentrations (50 mM), while in high NaCl concentration (100 and 150 mM), the improvement was observed on shoot system numbers. The fresh and dry weight results for both *cvs*. Masr 3 and Sakha 95 under saline and normal conditions are represented in Figure 5. As shown in Figure 5A, B, in absence of NaCl, the addition of AE-EH1 increased the dry weight by 13.89 % and 12.43 % in *cvs*. Masr 3 and Sakha95, respectively, while the highest improvement (%) under salt stressed samples were recorded in concentration of 150 mM and 100 mM of NaCl in *cv*. Sakha 95 (32.69 %) and *cv*. Masr 3 (13.72), respectively. On the other hand, the fresh weight results showed significant effect of PGP strain AE-EH1 on decreasing or even eliminating the salt stress on wheat plants (Figure 5C, D). As illustrated in Figure 5C, in absence of NaCl, treatment of *cv*. Sakha 95 with strain AE-EH1 led to an increase in the wheat plant fresh weight from 65.5 g/ pot to 96.43 g/ pot (32 %), while in *cv*. Masr 3, the increase in fresh weight was about 13.63 % under the same conditions (Figure 5D). Interestingly, the highest improvement value was recorded in *cv*. Sakha 95 at the highest NaCl concentration used (150 mM) with an increase of more than 60 % to reach 64.3 g/ pot, which was almost equal to that obtained in absence of NaCl (Figure 5C). On observing Figure 5, we can easily detect the significant positive impact of applying strain AE-EH1 on decreasing the effect of salt stress on both wheat cultivars.

Photosynthetic pigments: To find out the biochemical changes in wheat cultivars (Masr 3 and Sakha 95) treated with the PGP strain AE-EH1, some biochemical parameters were evaluated. Figure 6 shows the total content of some photosynthetic pigments, namely chlorophyll (a and b) and carotenoids in both *cvs*. Masr 3 and Sakha 95. The total contents of all the investigated pigments were severely decreased with increasing NaCl (150 mM) concentration compared to NaCl (0 mM) samples in both *cvs*. Masr 3 and Sakha 95 (Figure 6A, B). In response to strain AE-EH1 inoculation, chlorophyl a significantly increased by 70.2 %, 76.8 %, 114.2 %, and 244.5 % in control, 50, 100, and 150 mM NaCl in *cv*. Sakha 95 (Figure 6B), respectively, compared to the corresponding untreated samples. Similar results were obtained in *cv*. Masr 3, and the content of wheat chlorophyll a was increased by 59.3 %, 89.5 %, 114.6 %, and 118.1 % in control, 50, 100, and 150 mM NaCl, respectively, compared to the corresponding non-inoculated plants (Figure 6A).

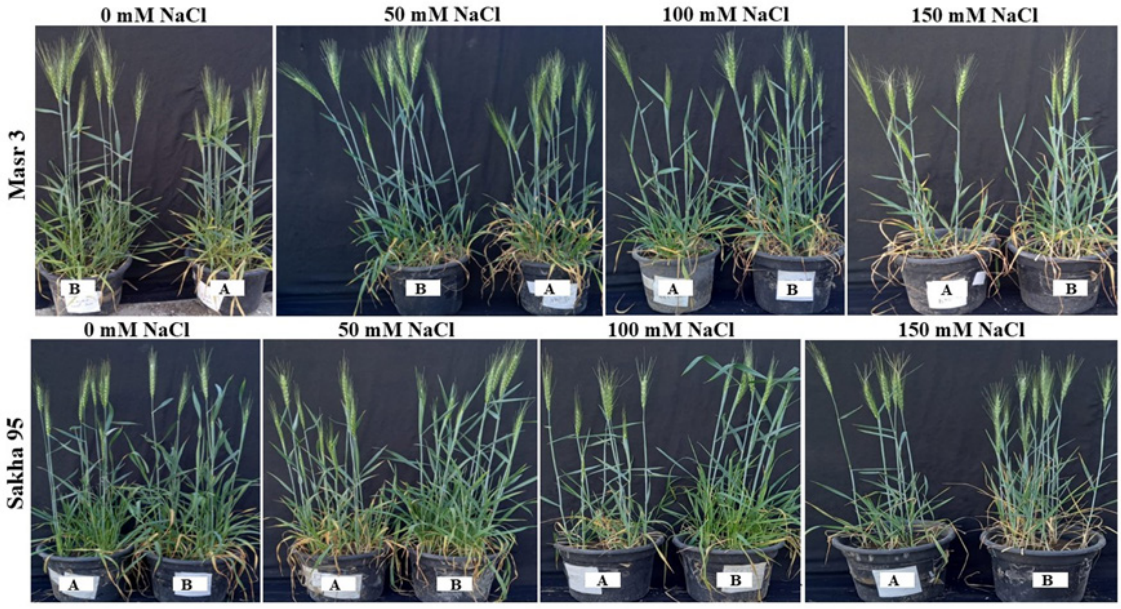

Figure 4: *The morphological features of Masr 3 and Sakha 95 wheat cultivars treated (B) and non-treated (A) with Baciluus sp. strain AE-EH1 upon treatment with different concentrations of NaCl (salt stress).*

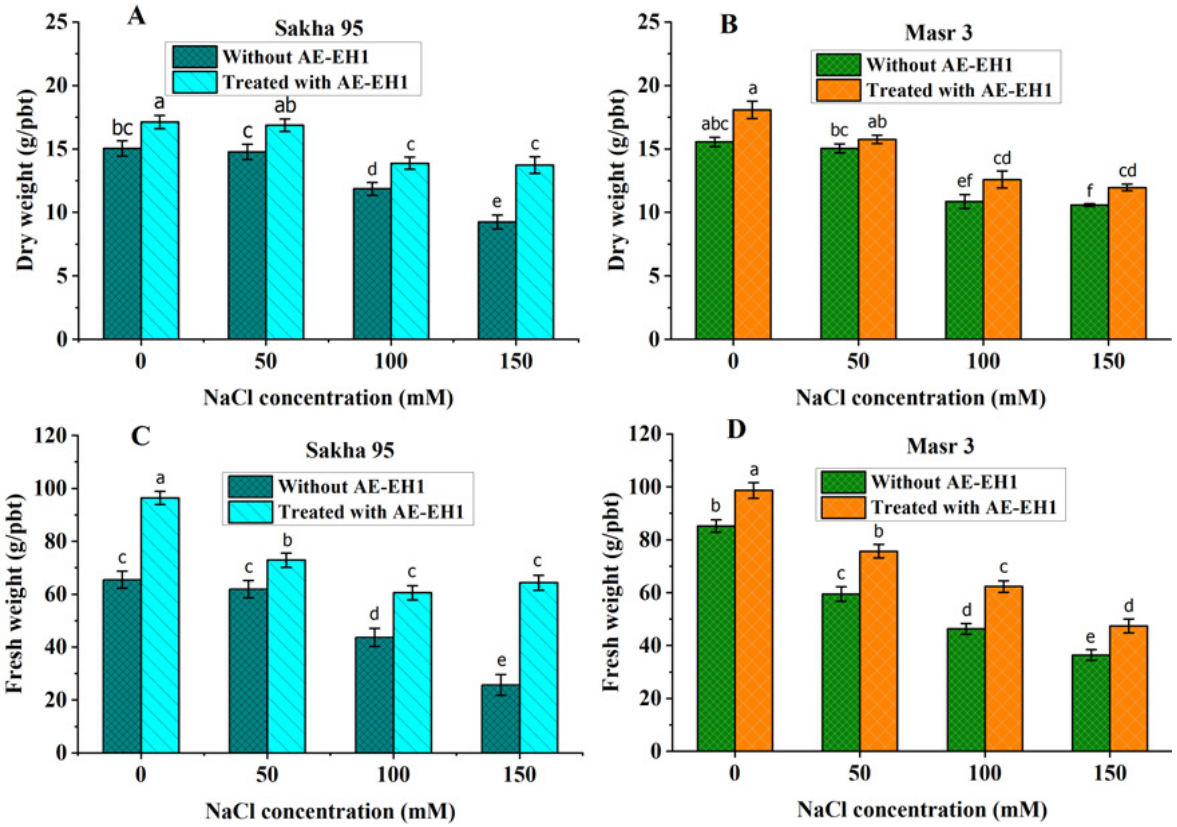

Figure 5: *Influence of salt-tolerant Bacillus sp. strain AE-EH1on dry weight (A, B) and fresh weight (C, D) of wheat phenotypes Sakha 95 (A, C) and Masr 3 (B, D). Error bars indicate the standard deviation (±SD) for three independent replicates. The different letters represent the means interaction significant differences at P ≤ 0.05.*

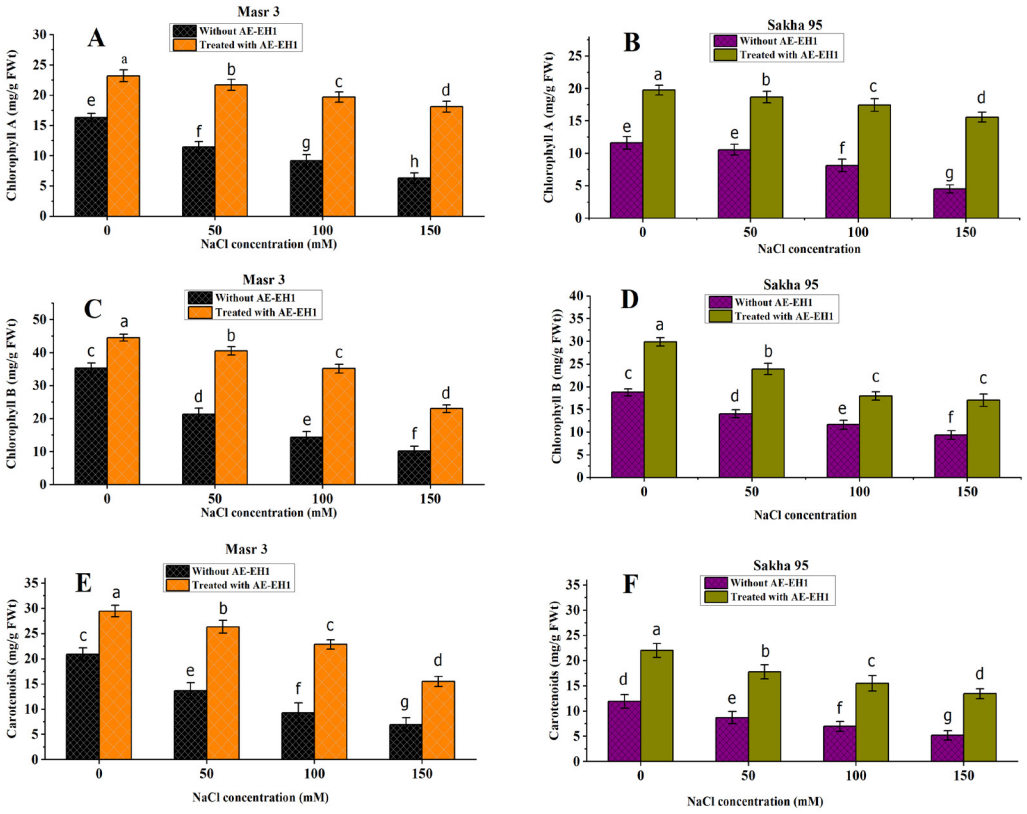

Figure 6: *Influence of salt-tolerant Bacillus sp. strain AE-EH1on chlorophyll A (A, B), chlorophyll B (C, D) and carotenoid (E, F) contents of two wheat phenotypes Masr 3 (A, C, E) and Sakha 95 (B, D, F). Error bars indicate the standard deviation (±SD) for three independent replicates. The different letters represent the means interaction significant differences at P ≤ 0.05.*

The same promising results were recorded for chlorophyll b. There was a severe decrease of chlorophyll b content from 35.2 and 18.9 mg/ g f wt to reach 10.2 and 23 mg/ g fwt, with increasing the salt stress in non-treated plants for both *cvs*. Masr 3 and Sakha 95, respectively (Figure 6C, D). The addition of strain AE-EH1 had a significant positive effect on increasing the amount of chlorophyll b. In *cv*..Masr 3, the increasing rate was 79.4 %, 89.8 %, 144.7 %, and 125.7 % for 0, 50, 100, and 150 mM NaCl, respectively, (Figure 6C). While, in *cv*. Sakha 95, the increasing rate was 95.7 %, 70.2 %, 54.2 %, and 81.2 % for 0, 50, 100 and 150 mM NaCl, respectively (Figure 6D).

Salt stress upon the selected wheat varieties caused a decrease in the content of carotenoid pigments with about 56.3 % and 66.6 % for *cv*. Sakha 95 and *cv*. Masr 3, respectively (Figure 6E, F). This decrease was recovered in those plants treated with PGP strain AE-EH1, where the increasing rate was 73.9 %, 92.4 %, 145.5 %, and 121.9 % in 0, 50, 100, and 150 mM NaCl in *cv*. Masr 3, respectively (Figure 6E), compared to the corresponding untreated plants. In *cv*. Sakha 95, the treated wheat plants recorded an increasing carotenoids rate of about 129.3 %, 104.1 %, 122.2 %, and 158.1% for 0, 50, 100, and 150 mM NaCl, respectively, compared to the corresponding untreated plants (Figure 6F).

Total contents of carbohydrates, proteins and lipids: Carbohydrate contents were significantly decreased under all levels of applied salt stress in both wheat cultivars (Figure 7A, B). However, the inoculation of strain AE-EH1 significantly improved the carbohydrate content. Maximum significant increase (50.25 %) was observed in concentration of 150 mM in *cv*. Sakha 95, while in *cv*. Masr 3, the highest improvement (50.6 %) was recorded at 100 mM, compared to the corresponding control without AE-EH1 inoculation (Figure 7A, B). As presented in Figure 7C, the total content of proteins in *cv*. Sakha 95 was highly improved by inoculation with strain AE-EH1. The total protein contents were 1.7, 1.2, 1.1, and 0.69 mg/g fwt in the treated plant samples compared to 1, 0.93, 0.55, and 0.28 in the untreated plant samples for 0, 50, 100, and 150 mM NaCl, respectively. Despite the high improvement in protein content in the *cv*. Sakha 95 inoculated plants; however, there was no significant improvement in the treated *cv*. Masr 3 plants (Figure 7D).

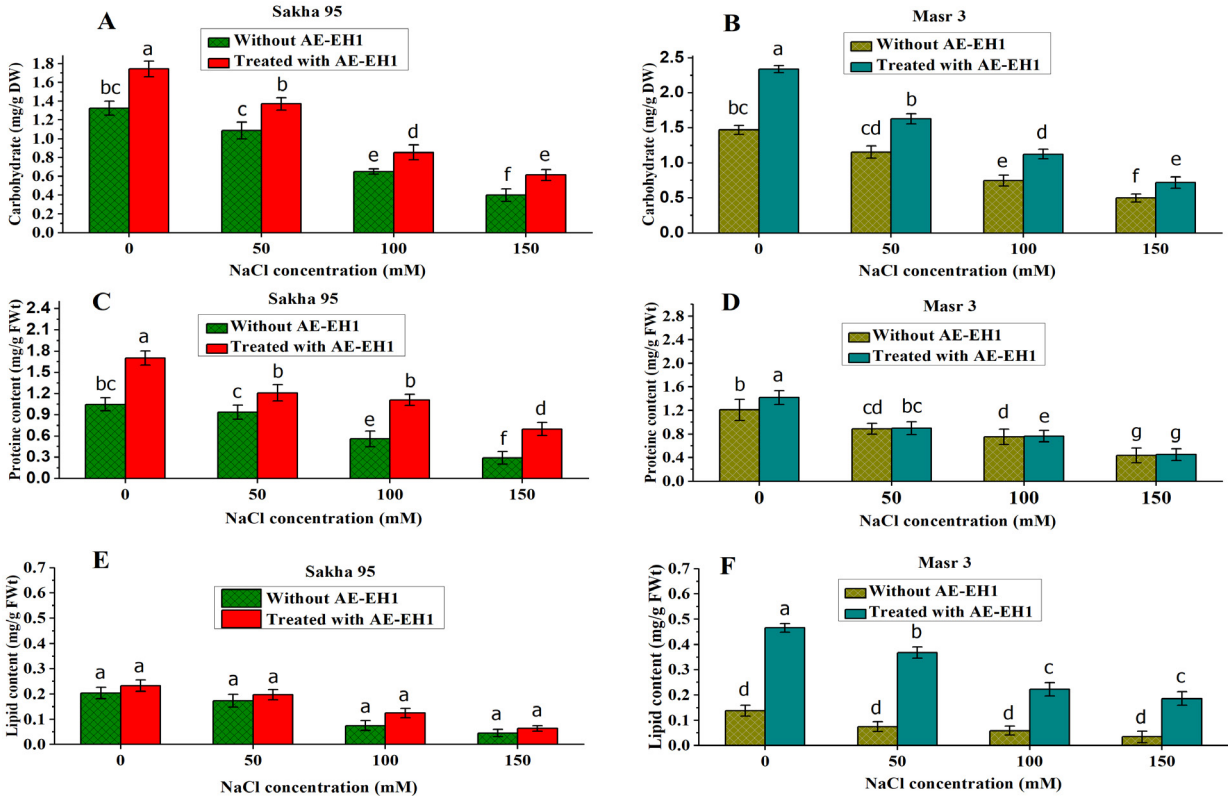

Figure 7: *Influence of salt-tolerant Bacillus sp. strain AE-EH1on carbohydrate (A, B), protein (C, D) and lipid (E, F) contents of two wheat phenotypes Sakha 95 (A, C, E) and Masr 3 (B, D, F). Error bars indicate the standard deviation (±SD) for three independent replicates. The different letters represent the means interaction significant differences at P ≤ 0.05.*

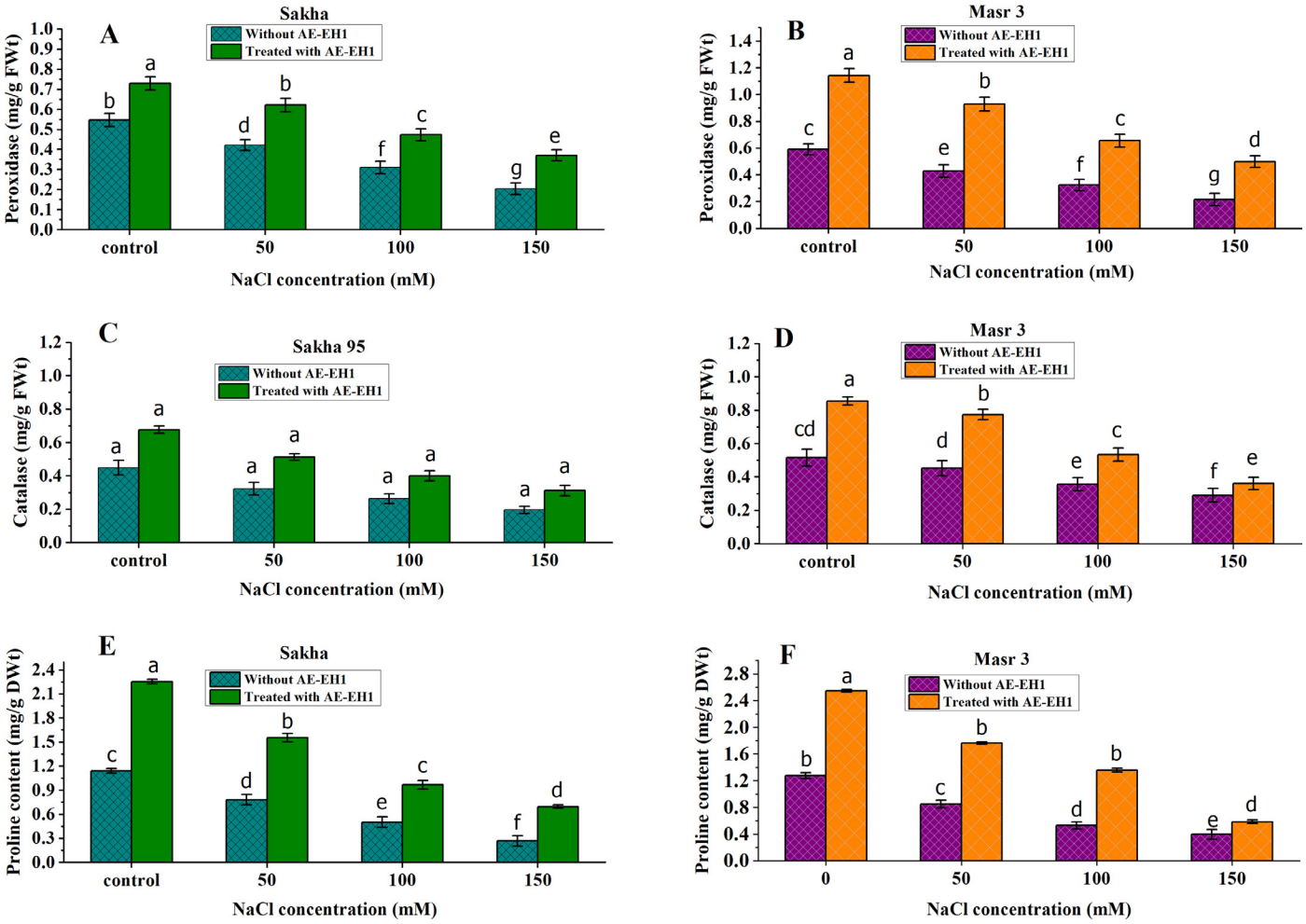

Figure 8: *Influence of salt-tolerant Bacillus sp. strain AE-EH1on peroxidase (A, B), catalase (C, D) and proline (E, F) contents of two wheat phenotypes Sakha 95 (A, C, E) and Masr 3 (B, D, F). Error bars indicate the standard deviation (±SD) for three independent replicates. The different letters represent the means interaction significant differences at P ≤ 0.05.*

For total lipids, the total amounts decreased significantly with increasing salt stress in both untreated *cvs*. Sakha 95 and Masr 3 wheat plants with decreasing the rate to 77.74 % in 150 mM NaCl, compared to the control without NaCl (Figure 7E, F). By inoculation with strain AE-EH1 to *cv*. Masr 3, the total amount of lipids was significantly increased to reach 0.42, 0.36, 0.22, and 0.19 mg/g fwt in 0, 50, 100, and 150 mM NaCl, respectively, compared to the corresponding NaCl concentrations without the inoculated bacterial strain (Figure 7F). The improvement of inoculation with strain AE-EH1 in *cv*. Sakha 95 was low compared to inoculation into *cv*. Masr 3, which recorded the highest value 0.19 mg/g fwt in 50 mM NaCl (Figure 7E).

Peroxidase, catalase and proline contents: The total contents of peroxidase, catalase, and proline in wheat plants are presented in Figure 8. The contents of peroxidase (Figure 8A, B) and catalase (Figure 8C, D) were dramatically decreased with increasing NaCl concentration in both *cvs*. Sakha 95 and Masr 3, inoculation with strain AE-EH1 improved the contents of both enzymes. For peroxidase enzyme, a noticeable improvement was observed (130±2.7 % and 81.24±3.0 %) in 150 mM NaCl in treated *cvs*. Masr 3 and Sakha 95, respectively, compared to corresponding non-treated plants. Despite the increase of peroxidase (significantly) and catalase (non-significantly) contents in inoculated *cv*. Sakha 95 (Figure 8A, C), *cv*. Masr 3 plants showed a better response to strain AE-EH1 inoculation. For catalase enzyme, non-significant improvement was detected in treated *cv*. Sakha 95 (Figure 8C) while treated *cv*. Masr 3 showed significant increase in catalase activity (65.41± 2.0, 70.80± 2.2, 49.92± 1.9, and 24.73± 1.8 %) with salt stress of 0, 50, 100, and 150 mM, respectively (Figure 8D). As illustrated in Figure 8E, F, proline accumulation in non-inoculated *cv*. Sakha 95 and *cv*. Masr 3 decreased with increasing salt stress. The

wheat *cvs*. Sakha 95 and Masr 3 treated with strain AE-EH1 expressed significant increase in proline content that was 2 and/or 3 times more in some NaCl concentrations, compared to its non-inoculated relevants. For *cv*. Masr 3, the highest increase in proline concentration (108± 2.2 and 156± 3.4 %) was recorded in pots with 50 and 100 mM NaCl respectively, while *cv*. Sakha 95 recorded 98.9± 2.9 and 158.4± 3.8 % increase in proline concentration in 50 and 150 mM NaCl, respectively.

Discussion

In the last decades marine derived bacteria have been attracted the scientists' attention due to their distinct phenotypic features and complex genetic coding comparing to the terrestrial partner. These properties improve their survival in such cruel conditions (Barzkar *et al*., 2024). Numerous studies have addressed the potential of marine derived bacteria or halo-bacteria in different industrial and agricultural aspects (Shan *et al*., 2023; Masmoudi *et al*., 2025). Soil salinity is a crucial environmental stress factor that negatively affects plant growth and productivity. Marine derived bacteria with salt tolerant capacity are the ideal choice to reinvigorate the plant growth under abiotic salt stress. They can adapt a wide range of environmental pressures, including salinity, temperature, acidity, and nutrient availability (Chbel *et al*., 2021). Marine derived bacteria can produce plant growth promoters that aid the plant to withstand the salt stress (Albdaiwi *et al*., 2019). In our study, all marine derived bacterial isolates were screened for their PGP traits. IAA is a phytohormone that orchestrate different plant process such as cell development and root initiation, therefore production of IAA by marine derived bacteria is crucial for plant physiology and productivity (Devi *et al*., 2024; Khalil *et al*., 2024). Here, all isolated strains showed positive results for IAA production ranging from (79.6 to 295.9 mg/ L). Our finding is in accordance with previous data reported by Orhan (2016), who isolated and identified eight halo-bacterial strains with IAA potential. Similarly, a previous study detected three halotolerant bacterial strains originating from saline habitats with IAA activity (Rupal *et al*., 2020).

Nitrogen fixation is a vital process that provides plants with nitrogen compounds, which in turn play a substantial role in normal growth and development (Zhang *et al*., 2019; Loveck *et al*., 2023). Halophilic bacteria can fix atmospheric N_2 similar to non-halophilic species (Orhan, 2021). In this study, only four isolates were able to fix N_2 while growing on NFM. For NH_4 production, all isolates were able to produce NH_4 ranging from 113.4to 646.7 mg/ l. NH_4 production by bacteria has been reported by Mehmood *et al*. (2021), as they identified a multifunctional *B. aryabhattai* strain PM34 with NH_4 production potential and other PGP activities. The bacterial strain *B. aryabhattai* PM34 was equipped with multiple PGP attributes, including N2 fixation, potassium and zinc solubilization, IAA, siderophore, and NH_4 production, along with various extracellular enzyme activities (Ali *et al*., 2009; Din *et al*., 2019, 2020).

Phosphorus is one of the essential plant nutrients (Khan *et al*., 2023). The percentage of phosphorus in soil is low and represents about 0.05 % (w/w); however, only 0.1 % of this value is available for plants. Some bacteria can solubilize soil phosphates into phosphorus giving benefits to the plants (Wang *et al*., 2022; Beltran-Medina *et al*., 2023). In this study, four isolates were able to solubilize phosphate. Among 31 bacterial isolates, we selected the most potent strain with PGP traits and identified as *Bacillus* sp. AE-EH1, based on classical approach and 16S rRNA gene sequencing. The genus *Bacillus* has been reported previously as PGP with salt tolerance capacity. Recently, two *Bacillus* strains, *B. subtilis* HG-15 and *B. velezensis* JC-K3 showed PGP efficacy (Ji *et al*., 2020, 2021). The PGP *B. frigoritolerans* can afford up to 10 % NaCl (Wang *et al*., 2021). *B. megaterium* NBRC 15308 and *Pseudomonas fluorescens* NBRC 14160 were growing upon 6 % salt concentration (Fathalla and El-Mageed, 2020). Currently, the target strain *Bacillus* sp. AE-EH1 tolerates and grows in high NaCl concentrations up to 15 % NaCl. Interestingly, growth of *Bacillus* sp. AE-EH1 was better in the presence of salt (3 % NaCl) compared to salt free medium. This implies that strain AE-EH1 not only tolerates high salt concentrations but also requires salt for maximum growth.

Bacteria have the capability to impede the growth of fungal pathogens through a variety of mechanisms, which encompass the production of antimicrobial substances, lytic enzymes such as chitinases, cellulases, β-1,3-glucanases, proteases, and lipases, and siderophores (Loveck *et al*., 2023). PGP that possess the ability to synthesize one or more of

these enzymes, which have been observed to exhibit biocontrol activity against several pathogenic fungi (Loveck *et al.*, 2023). The strain *Bacillus* sp AE-EH1 showed promising results against all tested plant pathogenic fungi. Earlier investigations have documented the antagonistic actions of PGP bacteria against several pathogenic fungi, such as *B. cinerea*, *S. rolfsii*, *F. oxysporum*, *R. solani*, *Pythium ultimum*, and the genus *Phytophthora* (Chávez-Ramírez *et al.*, 2020; Rahman *et al.*, 2025). Based on the unprecedented features of *Bacillus* sp. AE-EH1, we hypothesize that it could empower wheat plants upon abiotic salt stress.

Plant growth promoting bacteria can improve plants performance upon salt stress *via* regulating ion uptake to keep the balance between K^+/ Na^+ ratio, minimize the accumulation of Na^+ and Cl^- ions, and maintaining the level of macronutrients and micronutrients between plant and soil (Islam *et al.*, 2016; Etesami and Beattie, 2018). In the present study, treating two wheat *cvs*. Masr 3 and Sakha 95 with *Bacillus* sp. AE-EH1 increased their fresh and dry weights significantly in the absence of salt and upon gradual increase in salt stress. These findings support our hypothesis and propose the efficacy of PGP strain *Bacillus* sp. AE-EH1 to alleviating salt stress during wheat cultivation. Similarly, the dry weight of wheat cultivar Sakha 93 increased by 20 % during co-cultivation with PGP strains *Pseudomonas fluorescens* NBRC 14160 and *B. megaterium* NBRC 15308 (Fathalla and Abd El-Mageed, 2020). In another study, the multifunctional strain *B. aryabhattai* PM34 exhibited a strong potential as a PGP rhizobacterium capable of mitigating salt stress in wheat. *In vitro* inoculation of *B. aryabhattai* PM34 significantly improved seed germination, root length, shoot length, fresh biomass, and dry biomass under high-salinity conditions of 2 M NaCl (Mehmood *et al.*, 2021).

Photosynthetic pigments are the major player during energy generation in plants. However, their synthesis and performance are retarded upon salt stress, resulting in decreasing plant development and productivity (Fathalla and Abd El-Mageed, 2020). Salt stress suppress specific enzymes that involved in pigments biosynthesis along with reinvigoration of chlorophyllase action (Kaur *et al.*, 2014; Lu *et al.*, 2023). The total content of photosynthetic pigments, chlorophyll a, b and carotenoids were severely decreased in both *cvs*. Masr 3 and Sakha 95 in the presence of different NaCl concentrations. Interestingly, the effect of salt stress on wheat was recovered in both *cvs*. Masr 3 and Sakha 95 after treatment with *Bacillus* sp. AE-EH1. This finding indicates the potential role of our strain to support wheat plant and its pigments upon salt stress largely *via* production of PGP. Similarly, *B. aryabhattai* strain PM34 has been reported to elevate the content of chlorophyll during wheat germination under in the presence and absence of salt (Mehmood *et al.*, 2021). In the same context, co-cultivation of *Kocuria rhizophila* 14ASP and *Cronobacter sakazakii* OF115 led to increasing the content of photosynthetic pigments in wheat under salt concentration of 80–160 mM (Afridi *et al.*, 2019). Antioxidants are substances that can protect the plant cells from the oxidative damage of free radicals such as reactive oxygen species (ROS), which deteriorate the vital components in the cell (Fathalla and El-Mageed, 2020). Salinity can trigger the oxidative stress inside plant cells (Abd-Elgawad *et al.*, 2016; Aazami *et al.*, 2021). One of the strategies adopted by plant cells to alleviate the oxidative damage is up-regulation of intracellular antioxidant enzymes, such as peroxidase and catalase (Qi *et al.*, 2023; Ilyas *et al.*, 2024; Methela *et al.*, 2024). In this study, the levels of peroxidase and catalase were dramatically decreased with NaCl in both *cvs*. Sakha 95 and Masr 3. Interestingly, after treatment with *Bacillus* sp. AE-EH1, their levels were improved. Previous reports concluded that the level of peroxidase is up-regulated in salt resistant wheat cultivars and during co-cultivation with PGP bacteria (Fathalla and El-Mageed, 2020; Shahid *et al.*, 2022). Proline is an osmo-regulator that is accumulated inside plant cells as a routinely response to salt and drought stress (Hadid *et al.*, 2023). The level of proline has been recorded to increase in salt tolerant wheat cultivars comparing to sensitive ones (Poustini *et al.*, 2007; Aycan *et al.*, 2021; Hinai *et al.*, 2022). Our finding is compatible with several previous reports (Poustini *et al.*, 2007; Aycan *et al.*, 2021; Hinai *et al.*, 2022), whereas the proline content in treated wheat cultivars with *Bacillus* sp. AE-EH1 was high compared to non-treated plants under salt stress. This may be attributed to the inability of salt stressed wheat plants to synthesize the required proline owing to damages in their metabolic system. Our finding indicates the role of PGP *Bacillus* sp. AE-EH1 to improve wheat tolerance towards salt stress *via* increasing proline concentration.

Conclusions and Recommendations

The present study provides a bacterial strain *Bacillus*

sp. AE-EH1 possessing PGP traits, including production of IAA, NH_4, and HCN, as well as N_2 fixation and phosphate solubilization. The promising *Bacillus* sp. AE-EH1 displayed high salt tolerance, in addition to its *in vitro* antagonistic activity against 6 common phytopathogenic fungi. In the greenhouse, inoculating *Bacillus* sp. AE-EH1 into wheat plants (*cvs*. Sakha 95 and Masr 3) under salt stress resulted in significant reduction in salt stress effect in both cultivars by improving plant physiological characters. Interestingly, *Bacillus* sp. AE-EH1 is highly recommended to use for mitigation of salt stress in wheat plants. In addition, it can be used as a biocontrol and biofertilizer for wheat plants growing in healthy soil and/ or under abiotic saline stress.

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Novelty Statement

This study is the first to report the isolation and characterization of a marine-derived *Bacillus* sp. strain AE-EH1 (accession no. OR144427), exhibiting multifunctional PGP traits and halotolerance. Moreover, it demonstrated efficacy in enhancing the physiological, biochemical, and antioxidant responses of wheat *cvs*. Sakha 95 and Masr 3 under abiotic salt stress. The dual ability of *Bacillus* sp. strain AE-EH1 to mitigate salinity stress and suppress multiple phytopathogenic fungi underscores its potential as a novel and eco-friendly bio-inoculant for sustainable wheat cultivation in saline environments.

Author's Contribution

Eman Hamada: Conceptualization, research design, investigation, methodology, data analysis, writing of the original draft, and review and editing.
Adel Eltoukhy: Research design, investigation, methodology, data analysis, and review and editing.
Metwally K. Mahfouz: Methodology, and validation of results.
Abdel Kareem S.H. Mohamed: Supervision, validation of results, and review and editing.

Ethical approval
This study was conducted in accordance with ethical guidelines, and no human or animal subjects were involved. Ethical approval was not required for this research.

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Conflict of interests
The authors declare that there are no conflicts of interest.

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