

Synergistic Application of Marine-derived Actinomycetes and Microalgae to Enhance Rice Seedling Growth and Salinity Stress Tolerance

Alimuddin Ali^{1*}, Muhammad Junda¹, Nur Haedar², Hasliana¹,
Didik Imam Sakirin¹, and Herlina Rante³

¹Department of Biology, Faculty of Mathematics and Natural Science, Universitas Negeri Makassar, 90222 Makassar, South Sulawesi, Indonesia

²Department of Biology, Faculty of Mathematics and Natural Science, Hasanuddin University, 90245 Makassar, South Sulawesi, Indonesia

³Department of Pharmaceutical Sciences and Technology, Hasanuddin University, South Sulawesi, 90245 Makassar, South Sulawesi, Indonesia

ABSTRACT

Rice productivity on marginal land is significantly affected by salinity stress. However, biological approaches to improve rice growth tolerance remain insufficiently explored. This study aimed to evaluate the potential use of various actinomycete strains (SD 008, SD 021, SD 027), microalgae (*Chlorella* sp.), and their consortia to improve rice seedling growth and the physiological responses under different salinity levels (0, 50, and 100 mM NaCl). Rice seedling growth was assessed using several parameters, including seedling height, root length, number of roots, number of leaves, and biomass. In addition, the physiological condition of the plants was analysed using stress indicators consisting of chlorophyll *a* and *b* contents, proline, and malondialdehyde (MDA) accumulation. The results showed that treatment with strain SD 027 and the actinomycetes-microalgae

consortium had a significant effect on several growth parameters. This treatment was able to increase the germination index, maintain root development, and enhance chlorophyll content under moderate to high salinity conditions. Furthermore, the increase in proline content, coupled with a decreased MDA level, indicates an improvement in plant tolerance to oxidative stress. Our findings indicate that the combination of actinomycetes and microalgae provides a synergistic effect in enhancing rice seedling growth under salinity conditions. This approach has the potential to be developed as a more

ARTICLE INFO

Article history:

Received: 29 December 2024

Accepted: 09 March 2026

Published: 17 April 2026

DOI: <https://doi.org/10.47836/pjtas.49.2.07>

E-mail addresses:

muddin_69@unm.ac.id (Alimuddin Ali)

m.junda@unm.ac.id (Muhammad Junda)

nurhaedar@unhas.ac.id (Nur Haedar Nawir)

haslianalia19@gmail.com (Hasliana)

didik99imam@gmail.com (Didik Imam Sakirin)

herlinarante@unhas.ac.id (Herlina Rante)

* Corresponding author

environmentally friendly strategy to support plant growth on degraded land. However, further field trials are required to evaluate its effectiveness before it can be implemented in broader agricultural practices.

Keywords: Actinomycetes, MDA, microalgae, paddy seedling, proline, saline stress

INTRODUCTION

Salinity is one of the major abiotic stresses that significantly impairs crop productivity, particularly in rice (*Oryza sativa* L.) According to a 2021 report by the World Food Programme, millions of people in various countries still face severe levels of hunger (The World Food Programme, 2021). According to data from the Indonesian CBS in 2020, land conversion in Indonesia reaches 100,000 hectares annually, while the government's ability to open new rice fields is only around 40,000 hectares per year. Of the 189.1 million hectares of total land area in Indonesia, 157.2 million hectares consist of acidic soils, with the majority classified as dry acidic soils, accounting for approximately 108.8 million hectares or more than 60% of the total dry land in Indonesia. These types of soils are spread across almost all regions of Indonesia, from Kalimantan, Sumatra, parts of Sulawesi, to Papua (Centre Bureau of Statistics, 2020).

Suboptimal soils are characterised by reduced availability of essential macronutrients and elevated concentrations of toxic ions. The main issue with suboptimal land types is the reduction in nutrient solubility, particularly soluble phosphorus (P). Additionally, there is a decrease in the concentration of macroelements such as nitrogen (N), magnesium (Mg), calcium (Ca), and potassium (K), along with an increase in non-essential elements that can lead to plant toxicity (AbdelRahman et al., 2022). The efforts to improve the fertility of submarginal soils increasingly involve the use of microorganisms, which have become an important focus in sustainable agriculture research (Sadak & Dawood, 2023). Nitrogen-fixing bacteria, such as *Rhizobium* and *Azospirillum*, have long been reported to play a role in increasing nitrogen availability in submarginal soils. Several recent studies have also highlighted that these bacteria play an important role in supporting improved plant productivity in soils with low nitrogen content (Silva et al., 2022). The symbiosis between mycorrhizal fungi and plants has been recognised as contributing to the improvement of phosphorus availability and other essential nutrients in submarginal soils (Sadak, 2023). In addition, various studies have reported that actinomycetes and microalgae play an important role in enhancing plant growth under abiotic stress conditions. This role may occur through several biological mechanisms, including phytohormone production, nutrient Solubilisation, and modulation of the plant antioxidant system.

Several previous studies have indicated that the genus *Streptomyces* plays a role in enhancing plant tolerance to environmental stresses. Furthermore, microalgae have also

been reported to increase salt tolerance in tomato plants (*Solanum lycopersicum*) (Chen et al., 2025). Microalgae such as *Chlorella vulgaris* are also known to stimulate root elongation and shoot development in *Arabidopsis thaliana* under salinity stress by regulating proline accumulation and reactive oxygen species (ROS) levels (Fiorentino et al., 2025).

Various efforts have been undertaken to increase crop productivity through the application of modern agricultural technologies, including drainage systems, soil tillage, and the use of crop varieties that are tolerant to environmental stresses. Although these approaches provide certain benefits, their implementation often presents several challenges. One of the main limitations is the high financial investment required, which means that such technologies are not always accessible to smallholder farmers, particularly in developing countries (Midgley et al., 2017).

In addition, practices such as drainage and soil tillage may generate negative environmental impacts. Land degradation and disruption of natural ecosystems are among the long-term environmental impacts that may arise from these practices (Dai et al., 2022). Dependence on these technologies may also make farmers more vulnerable when these technologies become unavailable due to limited purchasing power or other supply constraints.

Microorganism-based approaches involving soil microbes have been widely reported as a key sustainable strategy to enhance environmentally friendly crop productivity. Actinomycetes and microalgae are groups of microorganisms with considerable potential for such applications. Actinomycetes are known for their ability to solubilise phosphate, fix atmospheric nitrogen, and produce various plant growth-promoting compounds such as indole-3-acetic acid (IAA). On the other hand, microalgae such as *Chlorella* sp. play an important role in increasing soil organic matter content, improving soil structure, and enhancing plant photosynthetic efficiency (Djebaili et al., 2020). The consortium of these two microorganisms is considered complementary, contributing to improved nutrient availability for plants (Bakhoun et al., 2023; Llamas et al., 2023).

The use of microbial consortia represents a highly promising approach in the development of more environmentally friendly and sustainable agricultural systems. This is closely related to the ability of microorganisms to reduce dependence on synthetic chemical fertilisers (Olanrewaju & Babalola, 2019). However, studies examining the interaction between locally derived tropical actinomycetes and microalgae as potential agents in the formulation of biostimulant technologies for improving submarginal soils remain very limited. This gap in scientific knowledge highlights the need for further exploration of the synergistic effects between these two groups of microorganisms, particularly regarding their role in improving soil health and enhancing crop productivity in tropical submarginal agricultural systems (Kusvuran, 2021).

The role of microorganisms in enhancing plant tolerance to various environmental stresses has been widely reported in previous studies. However, the interaction between actinomycetes and microalgae derived from tropical marine ecosystems has received relatively limited attention. Therefore, this study was designed to explore the potential of these microorganisms in improving the tolerance of rice seedlings to salinity stress during the early growth stage. Specifically, this research evaluates the effectiveness of actinomycetes isolates, both individually and in consortium with microalgae, in mitigating the negative effects of NaCl-induced salinity. The findings of this study are expected to contribute to the development of more sustainable biological approaches for enhancing rice resilience in environments with high salinity levels.

MATERIALS AND METHODS

Cultivation of Actinobacteria and Microalgae Strains

Selected actinomycete strains were rejuvenated on Starch Nitrate Agar (SNA) medium (prepared using seawater per litre of medium) for 7 days until spore formation occurred. Subsequently, each strain was cultured in starch nitrate broth (SN broth) by transferring an agar block (approximately 1.5 cm²) containing colonies from the SNA medium. The cultures were incubated on a shaker at an agitation speed of 150 rpm at 30 °C for 7 days. The culture broth was then transferred into ISP2 (International Streptomyces Project) fermentation medium at 10% (v/v) with a cell density of approximately 10⁷ cfu/mL for biomass production. The obtained biomass was washed three times with sterile distilled water to separate the biomass from the culture supernatant. The effects of actinomycetes and microalgae treatments on rice seed germination were evaluated through seed soaking under salinity stress conditions induced by NaCl at concentrations of 0, 50, and 100 mM. Seed germination responses were subsequently assessed at each level of salinity treatment.

In this study, microalgae of the genus *Chlorella* sp. were recovered from marine sponges and subsequently cultured in 300 mL of Walne medium contained in 1.5 L flasks under controlled laboratory conditions. The cultures were continuously aerated to ensure sufficient oxygen supply and proper mixing. A constant lighting system was maintained to provide continuous illumination for 24 hours throughout the experimental period. The cultures were incubated at room temperature for 7 days to allow the microalgae to grow and accumulate biomass optimally under these conditions.

Evaluation of Plant Growth-Promoting Potential

To assess the potential for plant growth-promoting properties, each isolate was tested for its ability to produce indole-3-acetic acid (IAA), solubilise phosphate, and nitrogen fixation. These tests were conducted to identify the functional characteristics of the isolates that play a role in supporting plant growth.

Indole-3-Acetic Acid (IAA) Production Activity

Indole-3-acetic acid (IAA) production in selected isolates was analysed to determine their potential plant growth-promoting activity. Each isolate was inoculated into ISP2 broth enriched with 0.5% tryptophan as a precursor for IAA biosynthesis. The cultures were then incubated at 30°C for 48-72 hours with shaking at 150 rpm to support microbial growth and metabolite production.

After the incubation period, the cultures were centrifuged at 10,000 rpm for 10 minutes to separate the bacterial cells from the culture supernatant. The supernatant was then used to determine IAA concentration using a colourimetric method with Salkowski's reagent, as described by Guardado-Fierros et al. (2024). For this purpose, 1 mL of the supernatant was mixed with 2 mL of Salkowski reagent, which consists of 2% ferric chloride (FeCl₃) in 35% perchloric acid. The mixture was then incubated in the dark at room temperature for 20-30 minutes until a pink colour formed, indicating IAA production. The intensity of the resulting colour was then measured using a spectrophotometer at a wavelength of 530 nm.

Phosphate Solubilisation Activity

Selected representative isolates were inoculated into the centre of Pikovskaya agar, a medium containing an insoluble phosphate source in the form of calcium phosphate (Ca₃(PO₄)₂). The culture plates were then incubated at 37°C for 7 days to allow sufficient time for microbial growth and the phosphate solubilisation process.

Phosphate solubilisation ability was observed through the formation of a clear zone (halo) around the microbial colony, indicating that the insoluble phosphate had been converted to a more soluble form. To increase data reliability, each test was performed in duplicate.

Furthermore, the solubilisation index (SI) was calculated quantitatively by comparing the total diameter, including the colony and the halo zone, to the colony diameter. This index calculation followed the method reported by Chakdar et al. (2018) using the following formula:

$$SI = \frac{\text{Total diameter (Colony + Halo zone)}}{\text{Colony diameter}}$$

Nitrogen Fixation Activity

The nitrogen fixation ability of selected isolates was evaluated using Burk's nitrogen-free medium with the following composition (g/L of distilled water): 10% glucose, 0.41% KH₂PO₄, 0.05% Na₂SO₄, 0.52% K₂HPO₄, 0.1% MgSO₄·7H₂O, 0.2% CaCl₂, 0.0025% Na₂MoO₄·2H₂O, 0.005% FeSO₄·7H₂O, and 15% agar, with the pH maintained at 7 ± 0.1. This medium is used to assess the ability of microorganisms to fix atmospheric nitrogen

because it does not contain an external nitrogen source. Evaluation was performed by inoculating isolates into Burk's nitrogen-free medium in either agar or broth form. For qualitative observation, isolates were streaked onto Burk N-free agar and then incubated at 30 °C for 5-7 days.

The ability of an isolate to grow in nitrogen-depleted media indicates potential nitrogen fixation activity. Furthermore, a blue colour change in the medium surrounding the colony serves as an additional indicator of the isolate's ability to fix atmospheric nitrogen.

Seed Viability Test

Rice (*Oryza sativa* L.) seeds were surface sterilised using 70% ethanol for 1 minute, then immersed in a 2% sodium hypochlorite solution for 10 minutes. Finally, the seeds were rinsed with sterile distilled water to remove any remaining sterilant. Seed viability was assessed using a germination test. Seeds were sown in Petri dishes containing moistened filter paper and incubated at room temperature for 7 days. Germination percentage was recorded to determine seed viability across different treatments. Germination was defined as the emergence of the radicle and endosperm. The germination of rice seeds was monitored and recorded daily to determine germination potential (%), germination rate (%), and the germination index. At the conclusion of the germination test, the radicle length, radicle thickness, and the length of young rice shoots were measured using a straightedge (Ullah et al., 2024).

Germination potential (%) was calculated using Equation 1:

$$GP = \frac{G2d}{Gt} \times 100 \quad [1]$$

where $G2d$ is the amount of germinated seeds in the first two days; Gt is the total amount of test seeds.

Germination rate (%) was calculated using Equation 2:

$$GE = \frac{Gf}{Gt} \times 100 \quad [2]$$

where Gf is the amount of germinated seeds when the seed reaches full germination; Gt is the total amount of test seeds.

Germination Index was calculated using Equation 3:

$$GI = \sum(Gt/Dt) \quad [3]$$

where Gt is the amount of germination on day t ; Dt is the corresponding amount of days to germination.

Growth Experiment

The experiment was conducted using rice seedlings grown under controlled laboratory conditions. Seeds were initially pre-germinated for 3 days in distilled water before being transferred to growth media containing NaCl concentrations of 0 mM (control), 50 mM, and 100 mM. Each treatment consisted of five groups: (1) control (no biological treatment), (2) strain SD 027, (3) strain SD 021, (4) strain SD 008, (5) microalgae, and (6) a consortium of actinomycetes with microalgae. Seedlings were grown for 14 days, and growth parameters, including seedling height, root length, root number, leaf number, and biomass, were recorded at the end of the experiment.

Chlorophyll Content of Paddy Seedlings

Chlorophyll *a* and *b* were extracted from fresh leaves using 80% acetone. Approximately 0.1 g sample of fresh leaves was first ground with acetone, then centrifuged at 10,000 rpm for 10 minutes to separate the chlorophyll extract from the residual leaf tissue. The resulting supernatant was then collected and analysed using a spectrophotometer, measuring absorbance at wavelengths of 663 nm for chlorophyll *a* and 645 nm for chlorophyll *b*.

Furthermore, chlorophyll content was calculated using the method proposed by Pérez-Patricio et al. (2018), and the results were expressed in mg/g fresh leaf weight.

$$\text{Chlorophyll } a \text{ (mg/g FW)} = (12.7 * A_{663}) - (2.59 * A_{645})$$

$$\text{Chlorophyll } b \text{ (mg/g FW)} = (22.9 * A_{645}) - (4.7 * A_{663})$$

The absorbance values, A_{663} and A_{645} , were recorded at wavelengths of 663 nm and 645 nm, respectively. The spectrophotometer was calibrated using an acetone/ethanol mixture.

Proline Accumulation Assay

The proline content of roots and leaves of paddy seedlings was measured following the procedure described by Gharsallah et al. (2016). Approximately 0.5 g of sample was ground and homogenised in 3% sulfosalicylic acid, then centrifuged at 3000 rpm for 10 minutes to separate the supernatant from the remaining tissue. The supernatant was mixed with acid-ninhydrin reagent and glacial acetic acid, then incubated at 100°C for 1 hour. The mixture was then extracted with toluene to extract the organic phase containing proline.

The absorbance of the toluene phase was measured at a wavelength of 520 nm using a spectrophotometer. Proline content was determined based on a standard curve, and the results were expressed as $\mu\text{mol/g}$ fresh weight.

Malondialdehyde (MDA) Analysis

Lipid peroxidation was assessed by measuring MDA content in roots and leaves as an indicator of oxidative stress (Patanè et al., 2022). Samples (0.5 g) were homogenised in 0.1% trichloroacetic acid (TCA) and centrifuged at 12,000 rpm for 15 minutes. The supernatant was mixed with 0.5% thiobarbituric acid (TBA) in 20% TCA and heated at 95°C for 30 minutes. After cooling, the mixture was centrifuged, and the absorbance was measured at 532 nm, 600 nm and 450 nm. MDA concentration was calculated using the extinction coefficient and expressed in nmol/g fresh weight.

$$\text{MDA (nmol/g FW)} = 6.45 \times (A_{532} - A_{600}) - 0.56 \times A_{450}$$

Morphological and Physiological Characterisation

The morphological and physiological characteristics of *actinomycetes* strains were determined using M1 growth media. Strains SD 008, SD 021, and SD 027 were morphologically characterised as Gram-positive filamentous bacteria and further identified through 16S rRNA gene sequencing. The gene was amplified using the universal primers 27F (5'-AGAGTTTGATCMTGGCTCAG-3') and 1492R (5'-TACGGYTACCTTGTTACGACTT-3').

The DNA sequences were edited and analysed using BioEdit, then aligned to reference sequences using ClustalW in MEGA11. Similarities to known organisms were checked using BLASTn in the NCBI GenBank database. A phylogenetic tree was then constructed using the neighbour-joining method, and branch reliability was validated using 1,000 bootstrap replicates.

The entire experimental workflow is depicted in a flowchart. This chart summarises the step-by-step evaluation of the effect of actinomycete and microalgae treatments on rice seedling growth under various levels of NaCl-induced salinity stress. The diagram also explains the inoculation process, salinity treatment, incubation period, and physiological and biochemical parameters measured at 14 days post-treatment (DAP) (Figure 1).

Data Analysis

Each experiment was conducted in triplicate to ensure the reliability of the results. The data obtained were analysed using one-way ANOVA, followed by a post-hoc Tukey test to evaluate significant differences between treatments. Results were considered statistically significant if $p < 0.05$.

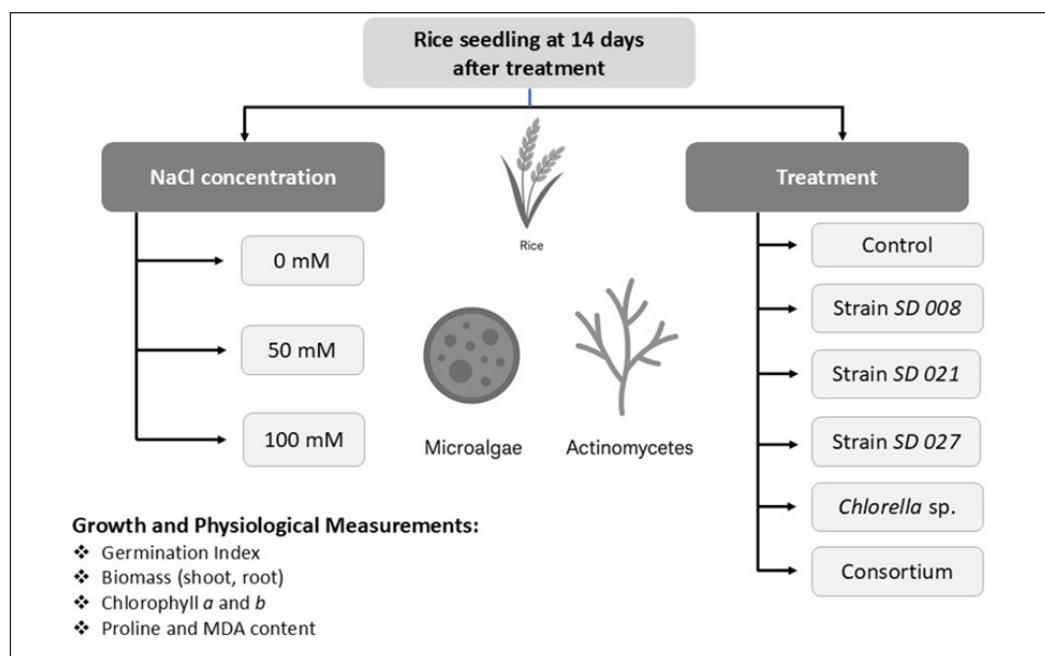


Figure 1. Flowchart of the experimental procedure for evaluating rice plant salt tolerance, microbial-induced

RESULTS AND DISCUSSION

Characteristic of Strains

Actinomycetes that were obtained from marine sponges exhibited morphological and physiological diversity when cultured in the laboratory. Substrate mycelium was observed in two distinct colours, brown and grey, while aerial mycelium showed a variety of colours ranging from yellowish brown to ivory white to pure white (Figure 2). These pigmentation patterns are consistent with the characteristics of the genus *Streptomyces*, which is known to produce a variety of pigments as secondary metabolites.

Optimal growth of the isolates was observed at 35-37 °C, indicating their adaptation to mesophilic conditions. Furthermore, the isolates also grew well at a neutral pH (pH 7), consistent with the pH conditions of their native marine environment (Table 1).

Regarding salinity tolerance, the isolates were able to grow in media containing 5-7% NaCl, confirming their halotolerant nature. This highlights the ability of marine actinomycetes to survive and thrive in habitats with moderate salt concentrations, a characteristic common among marine microbes.

Actinomycetes obtained from marine sponges exhibit unique morphological and physiological characteristics, most notably their spirally arranged spore chains.

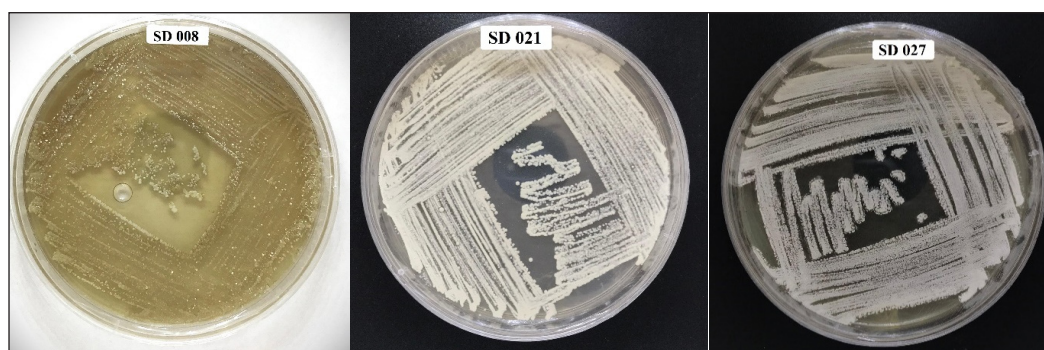


Figure 2. Morphological characteristics of the strain colony were grown on M1 medium (pH 7±0.2) at 30°C for 10 days

Table 1

The morphological and physiological traits of selective actinomycetes strains grown on different media

Parameter	Strain SD 008	Strain SD 021	Strain SD 027
Morphological characteristics			
Colony colour	Light brown	Ivory	White
Texture	Smooth	Powdery	Velvet
Aerial mycelium	Yellowish-brown	Ivory-white	White
Substrate mycelium	Brown	Brown	Grey
Spore chain ornament	Open coil spiral	Tight coil spiral	Open coil spiral
Pigmentation	Brown	-	-
Physiological characteristics			
Optimal growth temperature (°C)	35	35	37
Optimal pH for growth	7	7	8
Salt tolerance (%)	5	5	6

Note. All strains were grown on M1 medium (pH 7±0.2) at 30°C for 10 days

This characteristic is typically associated with the genus *Streptomyces*, known for its filamentous structure and spore-forming ability. The spiral arrangement of the spore chains facilitates the dispersal and survival of actinomycetes in marine environments, where nutrient availability and ecological pressures frequently fluctuate (Jackson et al., 2018; Riahi et al., 2019). Similar observations have been found in other marine actinomycetes, suggesting that this morphological adaptation provides advantages in colonisation and resilience in the complex sponge microhabitat (Jagannathan et al., 2021).

The dominant colony colours observed in actinomycetes isolated from marine environments, including sponges, are reflective of their adaptation to the oligotrophic and high-salinity conditions of the sea. In this study, most actinomycete colonies were white,

grey, and pale yellow. These colours are characteristic of *Streptomyces* species and have been widely documented in marine isolates (Naligama et al., 2022). Recent research has shown that actinomycetes associated with marine sponges often exhibit higher metabolic diversity compared to their terrestrial counterparts, as evidenced by their genomic and biosynthetic capabilities (Xu et al., 2023). Overall, the observed traits in actinomycetes, including spiral spore chains and dominant colony colours, are aligned with findings reported in recent marine microbiology studies.

Phylogenetic Tree Analysis of Strains

The 16S rDNA gene sequences of strains isolated from marine sponges were analysed to determine their phylogenetic relationships. BLAST analysis against the NCBI database revealed that all strains showed high sequence similarity to known species in the genus *Streptomyces* (Figure 3). The resulting phylogenetic tree indicated that the strains were closely related to *Streptomyces* species previously reported from marine environments. The nucleotide sequence differences observed among the isolates, despite their similarity to strains in the database, suggest that these strains may represent unique variants within the genus *Streptomyces*.

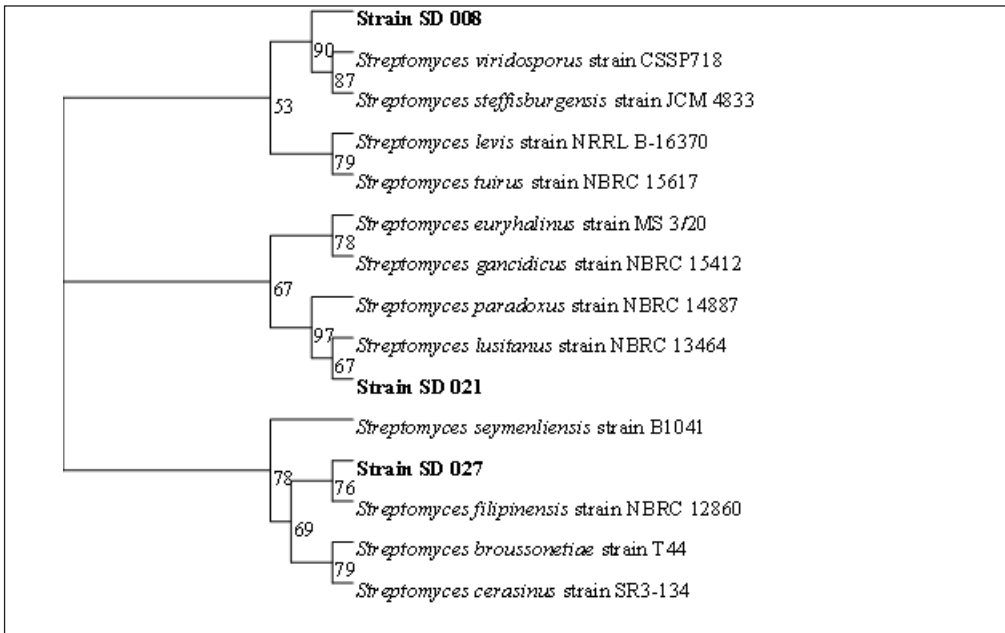


Figure 3. The phylogenetic relationships of strains isolated from marine sponges with related genera were inferred using the Neighbour-Joining method based on 16S rDNA gene sequences. Bootstrap values, calculated from 1000 replicates, are displayed as percentages at the branch points. The scale bar indicates 1 nucleotide substitution per 100 nucleotides

The phylogenetic analysis of strains isolated from marine sponges based on their 16S rDNA sequences revealed a close relationship to members of the genus *Streptomyces*. This genus is well-known for its remarkable diversity and its capacity to produce secondary metabolites with various biological activities, including antimicrobial and anticancer properties (Sarkar & Suthindhiran, 2022). The high bootstrap values observed in the phylogenetic tree confirmed the robustness of the clustering and the genetic relatedness of the strains to known *Streptomyces* species in the NCBI database. Previous studies have reported that *Streptomyces* genera often exhibit unique biosynthetic pathways and metabolic profiles, particularly when isolated from marine environments (Almeida et al., 2019). Marine *Streptomyces* strains are known for their remarkable adaptation to extreme marine conditions (Tangerina et al., 2020). The phylogenetic relationship of this isolate to other *Streptomyces* species is also consistent with findings reported in a similar study of actinomycetes from marine sponges (Chen et al., 2021).

Biological Activity of Strains

The ability of three actinomycete strains (SD 008, SD 021, and SD 027) to solubilise phosphate and produce indole-3-acetic acid (IAA) was evaluated to assess their potential as plant growth promoters. Phosphate solubilisation index (PSI) and IAA production values differed among the strains (Table 2). These differences in PSI values reflect the varying ability of each strain to release soluble phosphate from insoluble sources. The mechanism of phosphate solubilisation is primarily through the production of organic acids, which lower the pH of the surrounding medium and facilitate phosphate release (Boubekri et al., 2021). Strain SD 021, with the highest PSI (2.71), shows promising prospects as a phosphate-solubilising microorganism, indicating its strong capacity to increase phosphorus availability in the rhizosphere.

IAA production is an important plant growth-promoting trait, regulating root elongation, lateral root formation, and overall plant development. All three actinomycete strains exhibited significant IAA production, with strain SD 021 having shown the highest levels (116.21 µg/mL). The ability of these strains to synthesise large amounts of IAA highlights

Table 2

Physiological activity of selected actinomycete strains grown on M1 media

Strain	Phosphate Solubilisation [SI]	N ₂ -fixation	IAA Production (µg mL ⁻¹ ± SD)
SD 008	+ (1.52)	+	99.25±7.43
SD 021	++ (2.71)	+	116.21±6.44
SD 027	++ (2.11)	+	102.43±2.47

Note. The symbol + represents a positive reaction, - represents a negative reaction

their potential role in enhancing plant growth by promoting root system development and nutrient uptake (El-Bassiouny et al., 2020; Li et al., 2021).

The combination of phosphate solubilisation and IAA production in these strains represents a characteristic of marine *Streptomyces* species, which are often associated with enhanced plant growth. Previous studies have reported that *Streptomyces* spp. Isolated from marine environments, it not only tolerates extreme conditions but also contributes to plant growth under stress, such as saline soils or nutrient-deficient environments (Boukhatem et al., 2022; Romano-Armada et al., 2020).

Of the three actinomycetes strains, SD 021 showed higher biological activity in the process of phosphate solubilisation and IAA production. This suggests that SD 021 could be further explored as a biofertilizer candidate, particularly for improving crop productivity in nutrient-limited soils. However, additional *in planta* experiments are necessary to confirm these beneficial effects under field conditions.

Effect of Actinomycetes and Microalgae Treatments on Rice Seedlings Under NaCl Stress

Germination results under varying NaCl concentrations (0 mM, 50 mM, and 100 mM) revealed that the distilled water (control) treatment was consistently achieving the highest germination percentage (GP), average germination percentage (GE), and germination index (GI) across all conditions (Table 3) (Figure 4). Under the 0 mM NaCl treatment, control seeds were recorded to have reached GP, GE, and GI values of 95%, 95%, and 3.16, respectively. Moderate salinity (50 mM) was found to slightly reduce these values to 90%, 95%, and 3.16, while high salinity (100 mM) further decreased them to 85%, 100%, and 3.33.

Table 3
Response of rice seedlings under NaCl stress treated with actinomycetes and microalgae

Treatment	Seedling Percentage								
	0 mM NaCl			50 mM NaCl			100 mM NaCl		
	GP	GE	GI	GP	GE	GI	GP	GE	GI
Aquadest	95	95	3.16	90	95	3.16	85	70	3.33
SD 008	70	90	3	45	100	3.33	65	100	3.33
SD 021	70	80	2.6	40	95	3.16	20	65	2.16
SD 027	25	100	3.33	80	100	3.33	30	45	3
<i>Chlorella</i> sp.	65	90	3.33	60	85	2.8	35	80	2.67
SD+ <i>Chlorella</i> sp.	80	95	3	85	95	3.16	80	100	3.33

*GP, germination potential; GE, germination rate; GI, germination index

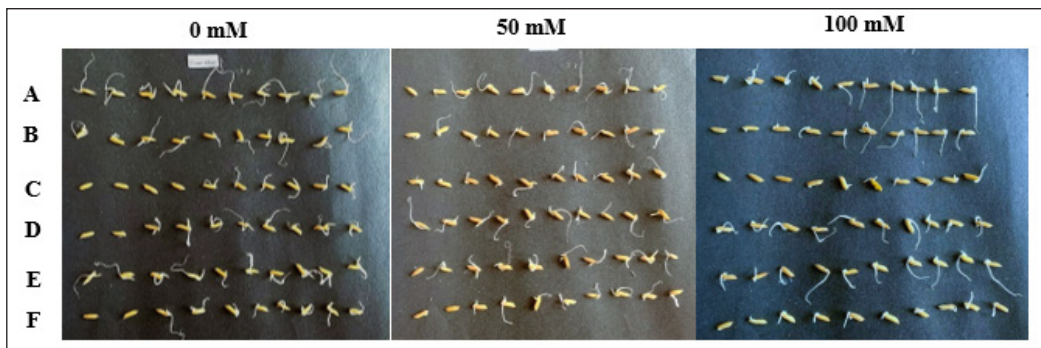


Figure 4. Growth profile of 14-day-old rice seedlings cultivated under NaCl stress conditions and treated with actinomycetes and microalgae

Note. Aquadest/water (A); SD 008 (B); SD 021 (C); SD 027 (D); *Chlorella* sp. (E); consortium of actinomycetes strains and microalgae SD+*Chlorella* sp. (F)

The combination of SD strains and microalgae was consistently observed to outperform individual treatments under stress conditions, resulting in GP, GE, and GI values of 80%, 100%, and 3.33 at 100 mM NaCl. This study highlights the potential of combining microbes and microalgae to promote seed germination under salinity stress.

Treatment with various actinomycetes was observed to show a positive effect on the germination ability of rice seeds under NaCl-induced stress at concentrations of 0, 50, and 100 mM (Figure 5). The results of this study indicate that microbial treatments, specifically strain SD 027 and the actinomycete-microalgae consortium, significantly improved rice seedling performance under saline conditions. At NaCl concentrations of 50 mM and 100 mM, the consortium was able to increase the germination index (GI) and maintain better root length and number compared to the control without treatment. These effects indicate a synergistic interaction between microalgae and actinomycetes. These effects are shown in increased photosynthesis and antioxidant production, while actinomycetes increase nutrient availability and produce phytohormones such as IAA. These findings are consistent with previous studies, which have shown that actinomycetes can enhance plant growth and stress tolerance by increasing nutrient availability, producing phytohormones, and inducing systemic resistance (Santoyo et al., 2021).

These findings are consistent with previous studies showing that actinomycetes and microalgae have been able to enhance seed germination by increasing nutrient availability and stress tolerance under favourable conditions (Msimbira et al., 2020). The beneficial effects of microbial consortia in mitigating salt stress, through mechanisms such as osmotic regulation and biofilm formation, have been widely reported (Xiong et al., 2019; Yujia et al., 2023). Our findings highlight the synergistic effect of combining actinomycetes and

microalgae, which was shown to enhance germination even under severe salinity stress, consistent with observations by Carillo et al. (2020). Although treatments with either actinomycetes or microalgae alone were able to produce positive effects, the combined application of both microorganisms significantly improved germination across a range of salinity levels. This enhanced performance is likely due to the microbes' ability to produce growth-promoting compounds, reduce oxidative stress, and maintain ion balance. Overall, these results support the reported evidence regarding the practical value of microbial consortia in managing agricultural systems under salinity stress (Ahluwalia et al., 2021).

Among microbial treatments, SD 008 and microalgae were demonstrated to have the potential to sustain germination under salt stress. At 100 mM NaCl, SD 008 was observed to maintain GE (100%) and GI (3.33) despite a lower GP (65%). Similarly, microalgae were found to achieve GE of 80% and GI of 2.67, but with a reduced GP (35%). Treatments with SD 027 and SD 021 were shown to exhibit diminished performance under increasing salinity, particularly at 100 mM, where GP dropped to 30% and 20%, respectively.

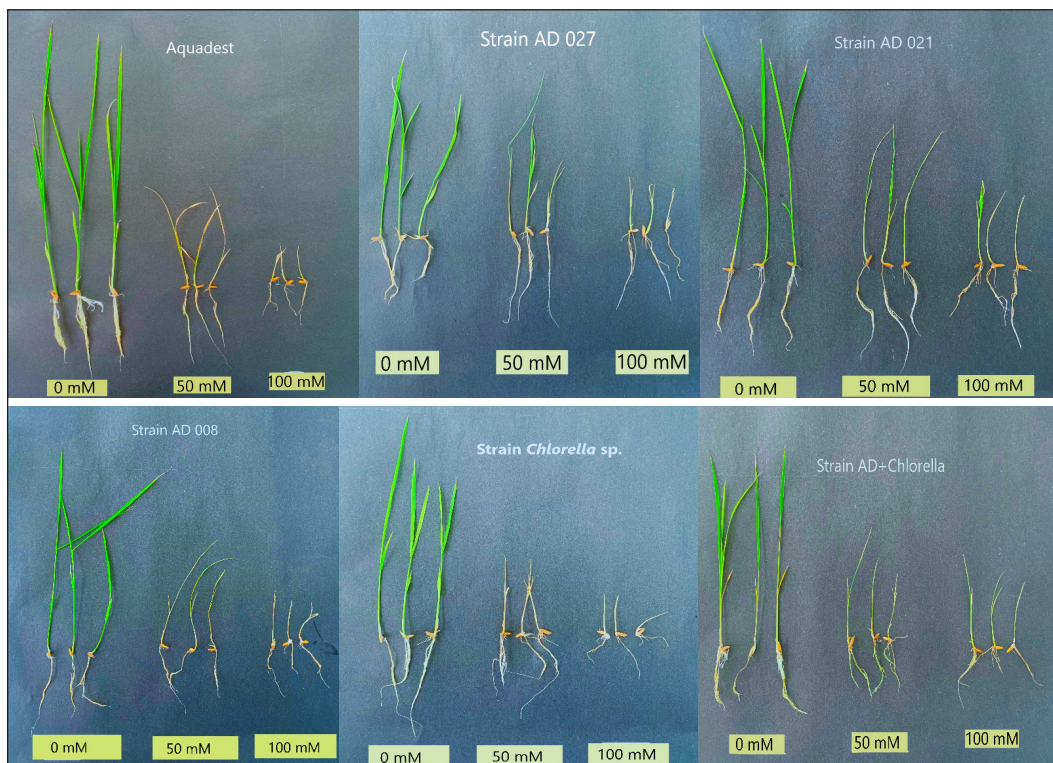


Figure 5. In vitro growth of rice seedlings under salinity levels (0, 50, and 100 mM NaCl) with actinomycetes and microalgae treatments at 14-day-old rice seedlings

Growth of Rice Seedlings In Vitro

Based on in vitro evaluation of rice seedlings after 14 days seedling height, root length, number of leaves, root count, and biomass under treatments with microbes and microalgae were measured at 0 mM, 50 mM, and 100 mM NaCl (Figure 4 and Figure 6)(Table 4) Under 0 mM NaCl, distilled water (control) produced the tallest seedlings (24.79 cm), but height declined sharply at 50 mM (9.58 cm) and 100 mM NaCl (4.74 cm). Microalgae showed the steepest height reductions, while SD 008 maintained moderate performance with smaller declines. Root length was longest with microalgae at 50 mM (7.40 cm) and with SD 027 at 100 mM (5.8 cm). Root count decreased with increasing salinity, but SD 027 and Actino + Microalgae were more effective in maintaining root growth than the control. SD 027 also increased leaf numbers by 30% under 50 mM NaCl, outperforming other treatments. Rice biomass weight showed a significant decrease at 100 mM NaCl concentration, although strain SD 027 was able to increase biomass at 50 mM concentration (0.080 g). This finding highlights the significant impact of salinity stress, but strain SD 027 has the effect of mitigating the negative impacts, especially at moderate salinity levels.

All the treatments were applied, and a consortium of microalgae and actinomycetes were proven to be the most effective in mitigating the negative impact of salinity on germination. Seeds treated with the consortium showed significantly higher germination

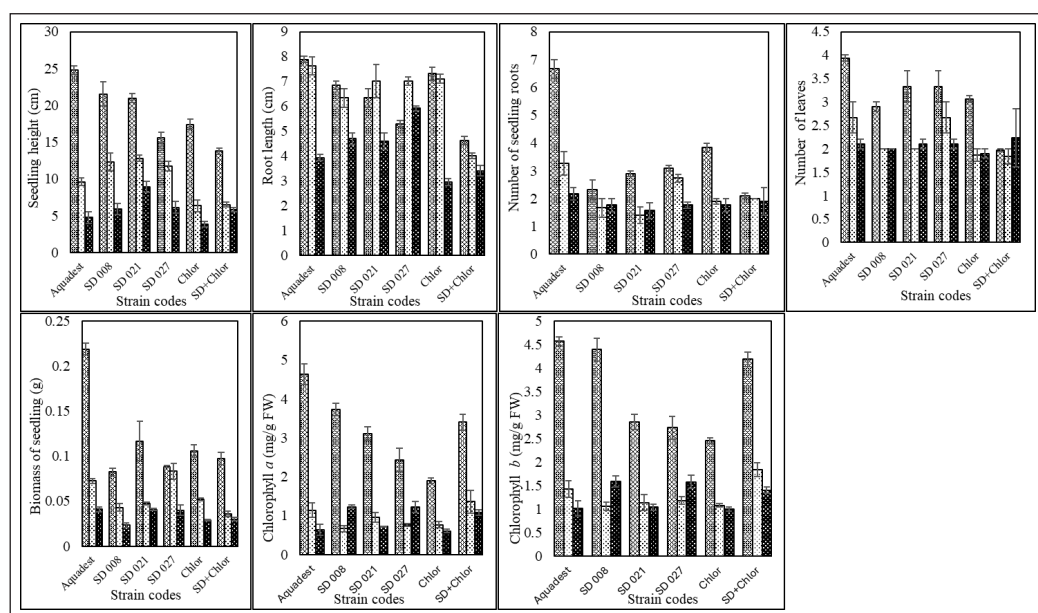


Figure 6. Growth response of 14-day-old *In Vitro* rice seedlings under salinity stress with Actinomycetes and microalgae treatments

Table 4
Response of 14-day-old *in vitro* rice seedlings under salinity stress with actinomycetes and microalgae treatments

Treatment	NaCl (mM)	Seedling Height	Root Length	No. of Roots	No. of Leaves	Biomass	Chl a (mg/g fw)	Chl b (mg/g fw)
Aquadest	0	24.786±0.996 ^a	7.881±0.219 ^a	6.666±0.577 ^a	3.933±0.115 ^a	0.219±0.011 ^a	4.630±0.459 ^d	4.570±0.165 ^b
	50	9.583±0.895 ^c	7.631±0.620 ^a	3.266±0.750 ^b	2.666±0.577 ^a	0.072±0.005 ^b	1.137±0.318 ^a	1.423±0.315 ^a
	100	4.743±1.321 ^d	3.933±0.231 ^b	2.166±0.378 ^b	2.101±0.173 ^a	0.041±0.004 ^c	0.637±0.244 ^a	1.513±0.480 ^a
SD 008	0	21.533±2.837 ^a	6.836±0.280 ^a	2.333±0.577 ^b	2.901±0.173 ^a	0.082±0.006 ^b	3.723±0.280 ^c	4.393±0.414 ^b
	50	12.311±2.089 ^b	6.333±6.333 ^a	1.666±0.577 ^b	2.000±0.000 ^a	0.043±0.007 ^c	0.663±0.143 ^a	1.060±0.156 ^a
	100	5.883±1.3194 ^d	4.691±0.420 ^b	1.766±0.404 ^b	2.000±0.000 ^a	0.023±0.005 ^c	0.441±0.545 ^a	0.936±0.733 ^a
SD 021	0	20.983±0.993 ^a	6.333±0.665 ^a	2.901±0.173 ^b	3.333±0.577 ^a	0.116±0.037 ^a	3.107±0.304 ^c	2.860±0.280 ^a
	50	12.793±0.718 ^b	7.016±1.167 ^a	1.401±0.529 ^b	2.000±0.000 ^a	0.047±0.002 ^c	0.950±0.219 ^a	1.133±0.290 ^a
	100	8.903±1.305 ^c	4.593±0.568 ^b	1.566±0.513 ^b	2.101±0.173 ^a	0.041±0.002 ^c	0.716±0.021 ^a	1.037±0.110 ^a
SD 027	0	15.600±1.241 ^b	5.281±0.235 ^a	3.111±0.173 ^b	3.333±0.577 ^a	0.088±0.001 ^b	2.437±0.525 ^b	2.733±0.418 ^a
	50	11.726±1.121 ^c	7.001±0.291 ^a	2.733±0.251 ^b	2.666±0.577 ^a	0.083±0.015 ^b	0.757±0.065 ^a	1.180±0.131 ^a
	100	6.136±1.354 ^d	5.923±0.170 ^a	1.766±0.208 ^b	2.101±0.173 ^a	0.041±0.011 ^c	0.176±0.025 ^a	1.033±0.072 ^a
<i>Chlorella</i> sp.	0	17.413±1.160 ^b	7.303±0.460 ^a	3.833±0.288 ^b	3.066±0.115 ^a	0.105±0.013 ^a	1.900±0.121 ^a	2.453±0.097 ^a
	50	6.340±1.421 ^d	7.096±0.315 ^a	1.901±0.173 ^b	1.866±0.231 ^b	0.052±0.002 ^c	0.767±0.132 ^a	1.077±0.035 ^a
	100	3.851±0.705 ^d	2.943±0.241 ^b	1.766±0.404 ^b	1.9±0.173 ^b	0.028±0.001 ^c	0.607±0.083 ^a	1.000±0.120 ^a
SD + Chlor	0	13.763±0.755 ^b	4.631±0.290 ^b	2.101±0.173 ^b	1.966±0.057 ^b	0.197±0.012 ^a	1.913±0.976 ^a	2.190±0.151 ^a
	50	10.591±0.341 ^b	4.011±0.196 ^b	2.000±0.011 ^b	1.833±0.288 ^b	0.035±0.005 ^c	1.357±0.515 ^a	1.840±0.256 ^b
	100	5.836±0.438 ^d	3.401±0.355 ^b	1.901±0.854 ^b	2.233±1.078 ^a	0.031±0.003 ^c	1.801±0.347 ^b	1.400±0.072 ^a

Data represent the mean values of three replicates ±SD. Different letters indicate a significant difference according to Tukey's post-hoc test at p<0.05

rates than seeds treated solely with microalgae, indicating a synergistic interaction between the two microorganisms in reducing salt stress. Microalgae were known to support plant growth by increasing photosynthetic efficiency and providing essential nutrients (García-González & Sommerfeld, 2016). In this study, the presence of actinomycetes in the consortium appeared to strengthen this effect, allowing the plant's stress tolerance mechanisms to function more optimally. Salinity stress has been shown to significantly affect rice growth through several mechanisms, such as disrupting water uptake, increasing plant growth, inducing ion toxicity, and producing oxidative stress (Chieb & Gachomo, 2023; Kumawat et al., 2022; Ragaey et al., 2022). A significant decrease in seedling height and root number correlated with increasing salinity. This is consistent with previous findings that salinity disrupts cell elongation and division (Abd El-Hameid & Sadak, 2020; Rodríguez et al., 2023). Treatment with distilled water (control) demonstrated the ability of plants to maintain optimal growth conditions at 0 mM NaCl but was unable to reduce the effects of salt stress at higher concentrations.

Treatment with strain SD 027 appears to have demonstrated its potential as a promising biostimulant, particularly in maintaining root length and biomass under high salinity conditions. Actinomycetes are known to increase plant tolerance to salinity through several mechanisms, including producing phytohormones, stabilising membrane integrity, and facilitating nutrient uptake (Inbaraj, 2021). Furthermore, the biological activity of strain SD 027 demonstrated a high phosphate solubilisation index and IAA production, potentially contributing to its effectiveness in mitigating the impact of salt stress. Similarly, strain SD 021 exhibited high phosphate solubilisation and IAA production, suggesting its potential role in increasing nutrient availability and stimulating root development (Jiang et al., 2019). Furthermore, strain SD 008, with a moderate phosphate solubilisation index and IAA production, demonstrated moderate performance under salinity stress. Importantly, all strains have been demonstrated to have nitrogen fixation capabilities, further supporting their role in nutrient cycling and plant growth under stressful environmental conditions.

Treatment with microalgae showed contrasting results, with a significant decrease in seedling height and biomass at higher salinity levels. This is likely due to the limited capacity of microalgae's bioactive compounds to withstand severe osmotic stress (Martínez-Ruiz et al., 2022). In contrast, the combination of actinomycetes and microalgae has been shown to have a synergistic effect, stabilising root and leaf growth, possibly through increased production of antioxidants and osmoprotectants (Fariza et al., 2024; Sultana et al., 2020). Biomass reduction under salinity stress is a common response in plants, associated with limited photosynthesis and impaired nutrient assimilation (Munns & Gilliam, 2015). In this study, strain SD 027 appeared to mitigate biomass loss, likely by regulating the expression of stress-responsive genes and maintaining cellular homeostasis (Abulfaraja & Jalal, 2021).

The differential response was observed among actinomycete strains at various salinity levels suggest that strain-specific traits play a crucial role in determining plant adaptation to salt stress. Overall, the findings of this study indicate that strains SD 027 and SD 021, as well as the combined application of actinomycetes and microalgae, have significant potential to mitigate the adverse effects of salinity on rice plants. To assess their practical application in agriculture, further research should be directed towards field trials and molecular analysis to better understand the mechanisms underlying the effectiveness of these biostimulants, particularly in soils affected by high salinity.

Chlorophyll Content Analysis

The results of chlorophyll content measurements in rice seedlings treated with microbes and grown at various NaCl concentrations (0, 50, and 100 mM) demonstrated significant physiological changes due to salinity stress. The control treatment with distilled water recorded the highest chlorophyll *a* content (4.6300 mg g⁻¹ wet weight), indicating optimal photosynthetic conditions. The response of plants treated with actinomycete strains SD 008 and SD 021 showed lower chlorophyll *a* content compared to the control, but did not differ significantly from each other, while the microalgae treatment produced the lowest value. All treatments at a concentration of 50 mM NaCl showed relatively uniform responses for chlorophyll *a* and *b*, with no significant differences. Interestingly, at 100 mM NaCl, the combination of actinomycetes and microalgae was able to significantly increase chlorophyll *a* content compared to other treatments, while chlorophyll *b* remained relatively constant in all treatments.

Chlorophyll *a* and *b* are essential components in the process of photosynthesis. The concentration levels of these two chlorophylls often indicate the physiological status of plants under environmental stress. Chlorophyll content decreased with increasing NaCl concentration. This corresponds to the inhibitory effect of salinity on photosynthesis, caused by ion imbalance, oxidative stress, and pigment degradation (Hameed et al., 2021; Sadak et al., 2022).

Meanwhile, the 0 mM NaCl treatment (control) showed high chlorophyll *a* levels. This effect is due to the absence of stress factors, allowing chlorophyll synthesis to proceed unimpeded. On the other hand, lower chlorophyll *a* levels were observed in the actinomycete treatments (SD 008 and SD 021). This is related to low physiological adaptation, although the two strains did not differ significantly from each other. Treatments with microalgae exhibited the lowest chlorophyll *a* levels, possibly due to resource competition or suboptimal fitness under these conditions (Kumar et al., 2020; O'Callaghan et al., 2022).

Furthermore, at 50 mM NaCl, there were no significant differences among treatments, suggesting a threshold effect where all treatments experienced a similar degree of stress-

induced decrease in chlorophyll synthesis. This study's findings align with previous research reporting that moderate salinity can induce similar physiological responses in plants (Etesami & Glick, 2020).

The effect of 100 mM NaCl concentration emphasised the potential synergistic effect of the consortium between actinomycete strains and microalgae in reducing high salinity stress. This synergy is thought to occur through complementary mechanisms. Increased nutrient uptake, reduced oxidative damage, or improved osmotic adjustment are mediated by interactions between microbes (Li et al., 2017). The absence of differences in chlorophyll *b* levels across all treatments indicates that salinity stress and microbial effects play a significant role in influencing the chlorophyll *a* biosynthesis pathway or its associated degradation mechanisms.

Overall, our findings highlight the potential application of microbial inoculants, particularly actinomycetes, and their combination to positively maintain chlorophyll levels under salinity stress. Further studies are recommended to explore the molecular and physiological mechanisms underlying these effects to optimize their application in agriculture on saline soils.

Proline is a crucial compound in plant physiological reactions. High proline content is widely used as a biochemical marker reflecting a plant's physiological ability to adapt to environmental stress. Environmental stress, particularly salinity, proline acts as an osmoprotectant and stabilises cellular structures (Dellero et al., 2020; El Moukhtari et al., 2020). Our findings demonstrate differences in rice root responses to NaCl-induced salinity stress under various microbial treatments.

Under saline conditions (0 mM NaCl), relatively high proline levels were observed in the control and SD 021 treatments. This indicates that these conditions support baseline proline synthesis for normal physiological function. Conversely, the significantly lower proline content in the SD 008 treatment indicates low proline biosynthetic activity. Furthermore, more efficient cellular homeostasis mechanisms are established when plants are not exposed to environmental stress. This evidence aligns with previous reports showing that proline accumulation is generally low when plants are not under environmental stress (Hosseinfard et al., 2022).

Meanwhile, at moderate salinity levels (50 mM NaCl), microalgae treatment was observed to stimulate a significant increase in proline accumulation. This is thought to be related to the microalgae's ability to produce extracellular metabolites, thus stimulating plants to overcome osmotic imbalances and maintain stress tolerance (Kishor et al., 2022). Furthermore, treatment with strain SD 008 also showed relatively high proline levels. This indicates its potential to stimulate the proline biosynthesis pathway, a physiological characteristic often found in high-salinity-tolerant actinomycetes (Ahammed et al., 2020; Sarsekeyeva et al., 2024).

Furthermore, in the 100 mM NaCl treatment, increased proline accumulation was found in both the microalgae treatment and the combination of microalgae and actinomyces. This may indicate a synergistic effect in alleviating high salinity stress. The effectiveness of microalgae is thought to be related to their ability to produce compatible compounds and antioxidant molecules. Meanwhile, actinomyces are thought to play a role in increasing nutrient uptake and maintaining ion balance within plant cells (Farfan-Cabrera et al., 2022). The opposite effect was observed, with the lowest proline content found in the control treatment under high salinity conditions. Negative effects of salt stress were observed when microbial treatments were not applied to protect plants from these unfavourable conditions. Overall, these results confirm that microbial inoculants play a key role in regulating proline metabolism, particularly in plants experiencing higher salinity stress. Furthermore, the combination of microalgae and actinomyces is considered a promising approach to increasing plant tolerance to salinity. Therefore, the molecular and biochemical interactions between the two require further investigation in future research.

Proline is a compound that plays a crucial role in plant physiology, functioning as an osmolyte, cytosolic pH regulator, antioxidant, and protein stabiliser (Khattab et al., 2024; Meena et al., 2019). This compound is crucial for plant adaptation mechanisms. It accumulates in plants when exposed to various abiotic stresses, such as salinity, drought, and extreme temperatures (Badr et al., 2025; Zhang et al., 2023). Several studies have shown that proline plays a role in maintaining osmotic balance, protecting cell structures, and reducing damage from oxidative stress (Nivedita et al., 2024). Interactions between microorganisms in consortia, including actinomyces and microalgae, have also been reported to increase plant tolerance to salinity. Increased proline accumulation, in response to reducing negative effects, is accompanied by improvements in overall plant physiological resilience (Mishra et al., 2021).

Proline also acts as an osmolyte to maintain cell water potential and prevent cellular dehydration under saline conditions. Furthermore, proline's involvement in signalling pathways that regulate plant responses to stress has been widely reported. This compound is known to interact with various proteins and enzymes, thus influencing the expression of genes related to stress tolerance. This is supported by metabolic adjustments to maintain energy balance when plants are exposed to unfavourable environments (Bakhroum et al., 2022; Renzetti et al., 2025). Proline protects against NaCl-induced oxidative damage by suppressing ROS accumulation and reducing lipid peroxidation. A relationship between increased proline accumulation and plant stress resistance has been demonstrated. Therefore, proline is used as a biomarker in plant breeding programs to improve salinity tolerance in various agricultural commodities (Elsawy et al., 2018).

Analysis of Proline Content

The analysis of proline content revealed considerable variation in proline accumulation across different treatments and NaCl concentrations (Table 5). Under non-saline conditions (0 mM NaCl), the control and strain SD 021 recorded the highest proline levels in the roots, reaching 12.3033 and 12.6367 nmol g⁻¹ fresh weight, respectively. In contrast, strain SD 008 exhibited the lowest proline concentration, at 2.9033 nmol g⁻¹.

At a moderate salinity level (50 mM NaCl), the microalgae treatment resulted in the highest proline accumulation (51.8633 nmol g⁻¹), which was significantly greater than that observed in the other treatments. A similar pattern was observed at 100 mM NaCl, where the microalgae treatment again showed the highest proline content (62.9933 nmol g⁻¹), followed by strain SD 027 (44.2733 nmol g⁻¹) and strain SD 008 (40.1867 nmol g⁻¹).

In addition, the combined application of microalgae and actinomycetes also led to a marked increase in proline accumulation under high salinity conditions. By contrast, the control exhibited the lowest proline level under the same conditions, with a value of 18.1000 nmol g⁻¹.

Analysis of MDA Content

The MDA (malondialdehyde) concentration increased with increasing salinity stress, indicating that oxidative stress in rice plants was enhanced (Table 6). Under non-saline conditions (0 mM NaCl), no significant differences were observed among the treatments, and the MDA levels were found to be relatively low. The lowest MDA concentration was recorded in strain SD 021, followed by strain SD 027, whereas the highest value was observed in strain SD 008.

Under moderate salinity stress (50 mM NaCl), the lowest MDA level was again recorded in the treatment with strain SD 021. An intermediate level of MDA was detected in the consortium treatment consisting of microalgae and actinomycetes, while a higher value was observed in the distilled water control.

At a higher salinity level (100 mM NaCl), clearer differences among the treatments were observed. Lower MDA levels were maintained in treatments with strains SD 008 and SD 021 compared with the distilled water control and the microalgae-actinomycetes consortium, in which the highest MDA concentrations were recorded.

Overall, the accumulation of MDA was consistently suppressed by strain SD 021 across different salinity levels, indicating that its potential role in reducing oxidative damage in rice plants can be suggested.

MDA is a compound widely recognised as a reliable indicator for detecting lipid peroxidation. The high accumulation of this compound in plant tissues is thought to reflect the extent of oxidative damage to cell membranes caused by abiotic stress (Sadak & Ramadan, 2021; Yu et al., 2020). Increased MDA levels were observed at higher NaCl

Table 5
In vitro proline content in roots and leaves of 14-day-old rice seedlings under salinity levels (0, 50, and 100 mM NaCl) with actinomycetes and microalgae treatments

Treatment	Proline Content (nmol g ⁻¹ Fresh Weight)					
	0 mM NaCl		50 mM NaCl		100 mM NaCl	
	Leaf	Root	Leaf	Root	Leaf	Root
Aquadest	10.403±1.130 ^c	12.303±0.915 ^c	14.393±1.955 ^b	33.080±2.0267 ^c	18.100±0.978 ^a	48.257±0.955 ^b
SD 008	12.273±2.059 ^c	2.903±0.688 ^a	20.173±2.045 ^c	26.480±0.6155 ^b	40.187±2.007 ^e	46.653±2.956 ^b
SD 021	3.640±0.605 ^a	12.637±1.708 ^c	18.247±2.639 ^c	20.990±1.9507 ^a	22.520±2.092 ^b	25.100±1.462 ^a
SD 027	6.413±1.047 ^b	5.543±0.783 ^b	21.340±1.262 ^c	26.103±0.773 ^b	44.273±1.046 ^d	48.213±0.607 ^b
<i>Chlorella</i> sp.	3.187±0.985 ^a	5.660±0.406 ^b	4.060±1.1191 ^a	51.863±2.590 ^e	34.140±1.985 ^c	62.993±2.482 ^c
SD+ <i>Chlorella</i> sp.	14.1767±1.161 ^d	5.704±0.764 ^b	20.197±1.970 ^c	39.127±1.361 ^d	39.793±3.484 ^e	49.297±0.861 ^b

Note. Data represent the mean values of three replicates ±SD. Different letters indicate a significant difference in proline content according to Tukey's post-hoc test at p<0.05

Table 6
In vitro MDA content in roots and leaves of 14-day-old rice seedlings under salinity levels (0, 50, and 100 mM NaCl) with actinomycetes and microalgae treatments

Treatment	MDA content X 10 ⁻⁵ (nmol g ⁻¹ fresh weight)					
	0 mM NaCl		50 mM NaCl		100 mM NaCl	
	Leaf	Root	Leaf	Root	Leaf	Root
Aquadest	3.72±0.62 ^a	1.60±0.12 ^a	2.49±0.54 ^c	5.73±0.10 ^c	19.60±4.00 ^a	7.23±0.42 ^b
SD 008	5.61±0.80 ^a	1.88±0.68 ^a	7.74±0.09 ^a	9.73±0.95 ^d	6.44±0.87 ^c	9.93±0.81 ^c
SD 021	3.57±0.15 ^a	1.91±0.01 ^a	8.19±0.36 ^a	1.33±0.040 ^a	8.39±0.63 ^c	4.89±0.30 ^a
SD 027	3.42±0.37 ^a	1.97±0.54 ^a	3.87±0.58 ^a	4.00±0.13 ^b	7.55±0.58 ^c	4.47±0.46 ^a
<i>Chlorella</i> sp.	1.88±0.76 ^b	2.77±0.15 ^a	1.34±0.29 ^b	5.71±0.13 ^c	14.17±0.52 ^b	5.25±0.80 ^a
SD+ <i>Chlorella</i> sp.	1.91±0.61 ^b	2.86±0.12 ^a	4.85±0.11 ^a	5.31±0.42 ^c	9.00±0.96 ^c	9.23±0.38 ^c

Note. Data represent the mean values of three replicates ±SD. Different letters indicate a significant difference in MDA content according to Tukey's post-hoc test at p<0

concentrations, and this trend is consistent with previous reports. Salinity stress can be associated with increased formation of reactive oxygen species (ROS), ultimately resulting in cell membrane damage (Narsing Rao et al., 2022).

In this study, consistently lower MDA levels were recorded in plants treated with strain SD 021, particularly at NaCl concentrations of 50 mM and 100 mM. These results indicate that this strain can be considered effective in reducing oxidative stress in plants. This effect is likely related to increased activity of antioxidant enzymes or production of osmoprotective compounds that may be induced by the SD 021 strain. This is in accordance with the results of studies that have been reported to contribute to increased plant tolerance under various stress conditions (Hegazy et al., 2023).

Interestingly, lower MDA concentrations were also observed in the microalgae-actinomycete consortium treatment compared to the control at 50 mM NaCl. However, its effectiveness was decreased at higher salinity levels, namely 100 mM NaCl. Microalgae are known to produce various bioactive compounds that play a role in increasing plant tolerance to stress. However, their effectiveness can be reduced at very high salinity levels, possibly due to limitations in maintaining cellular metabolic balance (Hamouda et al., 2022).

In contrast, MDA levels were maintained at a moderate range in plants treated with strain SD 027 across all salinity treatments, indicating that this strain can be considered to have a moderate capacity to suppress oxidative damage in plants.

Higher MDA concentrations were observed in plants treated with water under high salinity conditions, indicating the negative effects of uncontrolled ROS formation on plant growth and development. This study highlights the importance of selecting microbial treatments that are characterised by strong antioxidant properties to mitigate oxidative damage caused by stress. The ability of strain SD 021 to maintain lower MDA levels, even under high salinity conditions, was demonstrated in this study. These observations indicate that SD 021 can be considered a promising bioinoculant to improve the tolerance of rice plants to salt stress.

The findings obtained in this study indicate that a marine microbial consortium has the potential to be applied as a promising and environmentally friendly biofertiliser for agricultural lands affected by salinity. Although the results of this study were generated under *in vitro* conditions, a strong basis has been provided for further research. Therefore, further research needs to be conducted under field conditions and supported by molecular analysis to better understand the genetic and biochemical mechanisms involved in plant stress tolerance. In addition, the development of microbial biostimulants derived from locally isolated microorganisms is considered to have great potential to support more sustainable rice cultivation systems. This approach is expected to contribute to maintaining food security, particularly in marginal agricultural environments where salinity stress is common

CONCLUSION

Actinomycetes and microalgae isolated from marine environments have been shown to enhance rice seedling growth and improve plant tolerance to salinity. Oxidative stress levels in plants were reduced, indicating that the microbial treatment can support better physiological adaptation to salinity conditions. Among the tested strains, SD 027 was identified as the most effective under salinity stress.

Our findings suggest that the microbial consortium can be considered a promising and sustainable biostimulant for salinity-affected agricultural lands. However, further investigation under field conditions was needed to validate these findings in field conditions.

CONFLICTS OF INTEREST

The authors declare that they have no conflicts of interest.

ACKNOWLEDGMENT

This work was financially supported by the Indonesian Ministry of Research, Technology and Higher Education under grant PDKN DRTPM DIKTI 2024 No: 2841/UN36.11/LP2M/2024.

AI DISCLOSURE STATEMENT

The authors hereby declare that in preparing the manuscript, we used artificial intelligence (AI)-based tools for language editing was applied only to improve the clarity and fluency of the text.

This work represents the intellectual contributions of the authors and was prepared in accordance with the ethical standards of the journal.

REFERENCES

- Abd El-Hameid, A. R., & Sadak, M. S. (2020). Impact of glutathione on enhancing sunflower growth and biochemical aspects and yield to alleviate salinity stress. *Biocatalysis and Agricultural Biotechnology*, 29, Article 101744. <https://doi.org/10.1016/j.bcab.2020.101744>
- AbdelRahman, M. A. E., Metwaly, M. M., Afifi, A. A., D'Antonio, P., & Scopa, A. (2022). Assessment of soil fertility status under soil degradation rate using geomatics in West Nile Delta. *Land*, 11(8), Article 1256. <https://doi.org/10.3390/land11081256>
- Abulfaraja, A. A., & Jalal, R. S. (2021). Use of plant growth-promoting bacteria to enhance salinity stress in soybean (*Glycine max* L.) plants. *Saudi Journal of Biological Sciences*, 28(12), 3823-3834. <https://doi.org/10.1016/j.sjbs.2021.03.053>
- Ahammed, G. L., Li, X., Wan, H., Zhou, G., & Cheng, Y. (2020). *SIWRKY81* reduces drought tolerance by attenuating proline biosynthesis in tomato. *Scientia Horticulturae*, 270, Article 109444. <https://doi.org/10.1016/j.scienta.2020.109444>

- Ahluwalia, O., Singh, P. C., & Bhatia, R. (2021). A review on drought stress in plants: Implications, mitigation and the role of plant growth-promoting rhizobacteria. *Environmental Development and Sustainability*, 23(7), 9926-9948. <https://doi.org/10.1007/s10668-020-01003-y>
- Almeida, E. L., Carrillo Rincón, A. F., Jackson, S. A., & Dobson, A. D. W. (2019). Comparative genomics of marine sponge-derived *Streptomyces* spp. isolates SM17 and SM18 with their closest terrestrial relatives provides novel insights into environmental niche adaptations and secondary metabolite biosynthesis potential. *Frontiers in Microbiology*, 10, Article 1713. <https://doi.org/10.3389/fmicb.2019.01713>
- Badr, E. A., Bakhoun, G. S., Amin, G. A., & Sadak, M. S. (2025). Enhancing barley growth and yield under drought stress through exogenous folic acid application. *Egyptian Journal of Agronomy*, 47(1), 157-165. <https://doi.org/10.21608/agro.2025.310178.1485>
- Bakhoun, G., Amin, G. A., & Sadak, M. (2022). Biochemical study of some faba bean (*Vicia faba* L.) cultivars under different water regimes in sandy soil. *Egyptian Journal of Chemistry*, 65(132), 87-101. <https://doi.org/10.21608/ejchem.2022.117184.5288>
- Bakhoun, G. S., Tawfik, M. M., Kabesh, M. O., & Sadak, M. S. (2023). Potential role of algae extract as a natural stimulant for wheat production under reduced nitrogen fertiliser rates and water deficit. *Biocatalysis and Agricultural Biotechnology*, 51, Article 102794. <https://doi.org/10.1016/j.bcab.2023.102794>
- Boubekri, K., Soumare, A., Mardad, I., Lyamlouli, K., Hafidi, M., Ouhdouch, Y., & Kouisni, L. (2021). The screening of potassium- and phosphate-solubilising actinobacteria and the assessment of their ability to promote wheat growth parameters. *Microorganisms*, 9(3), Article 470. <https://doi.org/10.3390/microorganisms9030470>
- Boukhatem, Z. F., Merabet, C., & Tsaki, H. (2022). Plant growth-promoting actinobacteria, the most promising candidates as bioinoculants? *Frontiers in Agronomy*, 4, Article 849911. <https://doi.org/10.3389/fagro.2022.849911>
- Carillo, P., Ciarmiello, L. F., Woodrow, P., Corrado, G., Chiaiese, P., & Roupael, Y. (2020). Enhancing sustainability by improving plant salt tolerance through macro- and micro-algal biostimulants. *Biology*, 9(9), Article 253. <https://doi.org/10.3390/biology9090253>
- Central Bureau of Statistics. (2020). *The extent and distribution of critical land by province*. <https://www.bps.go.id/id/statistics-table/2/NTg4HzI=/luas-dan-penyebaran-lahan-kritis-menurut-provinsi.html>
- Chakdar, H., Dastager, S. G., Khire, J. M., Rane, D., & Dharne, M. S. (2018). Characterisation of mineral phosphate solubilising and plant growth-promoting bacteria from termite soil of an arid region. *3 Biotech*, 8(11), Article 463. <https://doi.org/10.1007/s13205-018-1488-4>
- Chen, J., Xu, L., Zhou, Y., & Han, B. (2021). Natural products from actinomycetes associated with marine organisms. *Marine Drugs*, 19(11), Article 629. <https://doi.org/10.3390/md19110629>
- Chen, Y., Ding, J., Wang, N., Ding, X., Wei, Y., Li, J., & Ding, G. C. (2025). Enhancing salt-stress tolerance in tomato (*Solanum lycopersicum*): The crucial role of bio-compost and rhizospheric *Luteimonas* spp. *Waste Management Bulletin*, 3(3), Article 100208. <https://doi.org/10.1016/j.wmbln.2025.100208>
- Chieb, M., & Gachomo, E. W. (2023). The role of plant growth-promoting rhizobacteria in plant drought stress responses. *BMC Plant Biology*, 23, Article 407. <https://doi.org/10.1186/s12870-023-04403-8>

- Dai, S., Ma, Y., & Zhang, K. (2022). Land degradation caused by construction activity: Investigation, cause and control measures. *International Journal of Environmental Research and Public Health*, *19*(23), Article 16046. <https://doi.org/10.3390/ijerph192316046>
- Dellero, Y., Clouet, V., Marnet, N., Pellizzaro, A., Dechaumet, S., Niogret, M. F., & Bouchereau, A. (2020). Leaf status and environmental signals jointly regulate proline metabolism in winter oilseed rape. *Journal of Experimental Botany*, *71*(6), 2098-2111. <https://doi.org/10.1093/jxb/erz538>
- Djebaili, R., Pellegrini, M., Smati, M., Del Gallo, M., & Kitouni, M. (2020). Actinomycete strains isolated from saline soils: Plant-growth-promoting traits and inoculation effects on *Solanum lycopersicum*. *Sustainability*, *12*(11), Article 4617. <https://doi.org/10.3390/su12114617>
- El Moukhtari, A., Cabassa-Hourton, C., Farissi, M., & Savouré, A. (2020). How does proline treatment promote salt stress tolerance during crop plant development? *Frontiers in Plant Science*, *11*, Article 1127. <https://doi.org/10.3389/fpls.2020.01127>
- El-Bassiouny, H. M. S., Abdallah, M. M., El-Enany, M. A. M., & Sadak, M. S. (2020). Nano-zinc oxide and arbuscular mycorrhiza effects on physiological and biochemical aspects of wheat cultivars under saline conditions. *Pakistan Journal of Biological Sciences*, *23*(4), 478-490. <https://doi.org/10.3923/pjbs.2020.478.490>
- Elsawy, H. I., Mekawy, A. M. M., Elhity, M. A., Abdel-dayem, S. M., Abdelaziz, M. N., Assaha, D. V., Ueda, A., & Saneoka, H. (2018). Differential responses of two Egyptian barley (*Hordeum vulgare* L.) cultivars to salt stress. *Plant Physiology and Biochemistry*, *127*, 425-435. <https://doi.org/10.1016/j.plaphy.2018.04.012>
- Etesami, H., & Glick, B. R. (2020). Halotolerant plant growth-promoting bacteria: Prospects for alleviating salinity stress in plants. *Environmental and Experimental Botany*, *178*, Article 104124. <https://doi.org/10.1016/j.envexpbot.2020.104124>
- Farfan-Cabrera, L. I., Franco-Morgado, M., González-Sánchez, A., Pérez-González, J., & Marín-Santibáñez, B. M. (2022). Microalgae biomass as a new potential source of sustainable green lubricants. *Molecules*, *27*(4), Article 1205. <https://doi.org/10.3390/molecules27041205>
- Fiorentino, S., Bellani, L., Santin, M., Castagna, A., Echeverria, M. C., & Giorgetti, L. (2025). Effects of microalgae as biostimulants on plant growth, content of antioxidant molecules and total antioxidant capacity in *Chenopodium quinoa* exposed to salt stress. *Plants*, *14*(5), Article 781. <https://doi.org/10.3390/plants14050781>
- García-González, M., & Sommerfeld, M. (2016). Biofertilizer and biostimulant properties of the microalga *Nannochloris* sp. on the growth of tomato plants. *Journal of Applied Phycology*, *28*, 3319-3328. <https://doi.org/10.1007/s10811-015-0625-2>
- Gharsallah, C., Fakhfakh, H., Grubb, D., & Gorsane, F. (2016). Effect of salt stress on ion concentration, proline content, antioxidant enzyme activities and gene expression in tomato cultivars. *AoB PLANTS*, *8*, Article plw055. <https://doi.org/10.1093/aobpla/plw055>
- Guardado-Fierros, B. G., Tuesta-Popolizio, D. A., Lorenzo-Santiago, M. A., Rodriguez-Campos, J., & Contreras-Ramos, S. M. (2024). Comparative study between Salkowski reagent and chromatographic method for auxins quantification from bacterial production. *Frontiers in Plant Science*, *15*, Article 1378079. <https://doi.org/10.3389/fpls.2024.1378079>

- Hameed, A., Ahmed, M. Z., Hussain, T., Aziz, I., Ahmad, N., Gul, B., & Nielsen, B. L. (2021). Effects of salinity stress on chloroplast structure and function. *Cells*, *10*(8), Article 2023. <https://doi.org/10.3390/cells10082023>
- Hamouda, R., Shehawy, M., Mohy El Din, S., Albalwe, F., Albalawi, H., & Hussein, M. (2022). Protective role of *Spirulina platensis* liquid extract against salinity stress effects on *Triticum aestivum* L. *Green Processing and Synthesis*, *11*(1), 648-658. <https://doi.org/10.1515/gps-2022-0065>
- Hegazy, G. E., Olama, Z. A., Abou-Elela, G. M., & others. (2023). Biodiversity and biological applications of marine actinomycetes—Abu-Qir Bay, Mediterranean Sea, Egypt. *Journal of Genetic Engineering and Biotechnology*, *21*, Article 150. <https://doi.org/10.1186/s43141-023-00612-8>
- Hosseini-fard, M., Stefaniak, S., Ghorbani Javid, M., Soltani, E., Wojtyła, Ł., & Garnczarska, M. (2022). Contribution of exogenous proline to abiotic stresses tolerance in plants: A review. *International Journal of Molecular Sciences*, *23*(9), Article 5186. <https://doi.org/10.3390/ijms23095186>
- Inbaraj, M. P. (2021). Plant-microbe interactions in alleviating abiotic stress: A mini review. *Frontiers in Agronomy*, *3*, Article 667903. <https://doi.org/10.3389/fagro.2021.667903>
- Jackson, S. A., Crossman, L., Almeida, E. L., Margassery, L. M., Kennedy, J., & Dobson, A. D. W. (2018). Diverse and abundant secondary metabolism biosynthetic gene clusters in the genomes of marine sponge-derived *Streptomyces* spp. isolates. *Marine Drugs*, *16*(2), Article 67. <https://doi.org/10.3390/md16020067>
- Jagannathan, S. V., Manemann, E. M., Rowe, S. E., Callender, M. C., & Soto, W. (2021). Marine actinomycetes, new sources of biotechnological products. *Marine Drugs*, *19*(7), Article 365. <https://doi.org/10.3390/md19070365>
- Jiang, H., Wang, T., Chi, X., Wang, M., Chen, N., Chen, M., Pan, L., & Qi, P. (2019). Isolation and characterisation of halotolerant phosphate-solubilising bacteria naturally colonising the peanut rhizosphere in salt-affected soil. *Geomicrobiology Journal*, *37*(2), 110-118. <https://doi.org/10.1080/01490451.2019.1666195>
- Khattab, H. I., Sadak, M. S., Dawood, M. G., Elkady, F. M. A., & Helal, N. M. (2024). Foliar application of esculin and digitoxin improve the yield quality of salt-stressed flax by improving the antioxidant defense system. *BMC Plant Biology*, *24*, Article 963. <https://doi.org/10.1186/s12870-024-05626-z>
- Kishor, P. B. K., Suravajhala, P., Rathnagiri, P., & Sreenivasulu, N. (2022). Intriguing role of proline in redox potential conferring high-temperature stress tolerance. *Frontiers in Plant Science*, *13*, Article 867531. <https://doi.org/10.3389/fpls.2022.867531>
- Kumar, A., Singh, S., Gaurav, A. K., Srivastava, S., & Verma, J. P. (2020). Plant growth-promoting bacteria: Biological tools for the mitigation of salinity stress in plants. *Frontiers in Microbiology*, *11*, Article 1216. <https://doi.org/10.3389/fmicb.2020.01216>
- Kumawat, C., Kumar, A., Parshad, J., Sharma, S. S., Patra, A., Dogra, P., Yadav, G. K., Dadhich, S. K., Verma, R., & Kumawat, G. L. (2022). Microbial diversity and adaptation under salt-affected soils: A review. *Sustainability*, *14*(15), Article 9280. <https://doi.org/10.3390/su14159280>
- Kusvuran, S. (2021). Microalgae (*Chlorella vulgaris* Beijerinck) alleviates drought stress of broccoli plants by improving nutrient uptake, secondary metabolites, and antioxidative defense system. *Horticultural Plant Journal*, *7*(3), 221-231. <https://doi.org/10.1016/j.hpj.2021.03.007>

- Li, H., La, S., Zhang, X., Gao, L., & Tian, Y. (2021). Salt-induced recruitment of specific root-associated bacterial consortium capable of enhancing plant adaptability to salt stress. *The ISME Journal*, *15*, 2865-2882. <https://doi.org/10.1038/s41396-021-00974-2>
- Li, H. Q., & Jiang, X. W. (2017). Inoculation with plant growth-promoting bacteria (PGPB) improves salt tolerance of maize seedling. *Russian Journal of Plant Physiology*, *64*, 235-241. <https://doi.org/10.1134/S1021443717020078>
- Llamas, A., Leon-Miranda, E., & Tejada-Jimenez, M. (2023). Microalgal and nitrogen-fixing bacterial consortia: From interaction to biotechnological potential. *Plants*, *12*(13), Article 2476. <https://doi.org/10.3390/plants12132476>
- Martínez-Ruiz, M., Martínez-González, C. A., Kim, D. H., Santiesteban-Romero, B., Reyes-Pardo, H., Villaseñor-Zepeda, K. R., Meléndez-Sánchez, E. R., Ramírez-Gamboa, D., Díaz-Zamorano, A. L., Sosa-Hernández, J. E., Coronado-Apodaca, K. G., Gámez-Méndez, A. M., Iqbal, H. M. N., & Parra-Saldivar, R. (2022). Microalgae bioactive compounds to topical applications products: A review. *Molecules*, *27*(11), Article 3512. <https://doi.org/10.3390/molecules27113512>
- Meena, M., Divyanshu, K., Kumar, S., Swapnil, P., Zehra, A., Shukla, V., Yadav, M., & Upadhyay, R. S. (2019). Regulation of L-proline biosynthesis, signal transduction, transport, accumulation, and its vital role in plants during variable environmental conditions. *Heliyon*, *5*(12), Article e02952. <https://doi.org/10.1016/j.heliyon.2019.e02952>
- Midgley, S. J., Stevens, P. R., & Arnold, R. J. (2017). Hidden assets: Asia's smallholder wood resources and their contribution to supply chains of commercial wood. *Australian Forestry*, *80*(1), 10-25. <https://doi.org/10.1080/00049158.2017.1280750>
- Mishra, P., Mishra, J., & Arora, N. K. (2021). Plant growth-promoting bacteria for combating salinity stress in plants - Recent developments and prospects: A review. *Microbiological Research*, *252*, Article 126861. <https://doi.org/10.1016/j.micres.2021.126861>
- Msimbira, L. A., & Smith, D. L. (2020). The roles of plant growth-promoting microbes in enhancing plant tolerance to acidity and alkalinity stresses. *Frontiers in Sustainable Food Systems*, *4*, Article 106. <https://doi.org/10.3389/fsufs.2020.00106>
- Munns, R., & Gilliham, M. (2015). Salinity tolerance of crops - What is the cost? *New Phytologist*, *208*(3), 668-673. <https://doi.org/10.1111/nph.13519>
- Naligama, K. N., Weerasinghe, K. E., & Halmillawewa, A. P. (2022). Characterisation of bioactive actinomycetes isolated from Kadolkele mangrove sediments, Sri Lanka. *Polish Journal of Microbiology*, *71*(2), 191-204. <https://doi.org/10.33073/pjm-2022-017>
- Narsing Rao, M. P., Lohmaneeratana, K., Bunyoo, C., & Thamchaipenet, A. (2022). Actinobacteria-plant interactions in alleviating abiotic stress. *Plants*, *11*(21), Article 2976. <https://doi.org/10.3390/plants11212976>
- Nivedita, S., Behera, S. S., Behera, P. K., Parwez, Z., Giri, S., Behera, H. T., & Ray, L. (2024). Salt-resistant *Streptomyces* consortia promote growth of rice (*Oryza sativa* var. Swarna) alleviating salinity and drought stress tolerance by enhancing photosynthesis, antioxidant function, and proline content. *The Microbe*, *4*, Article 100124. <https://doi.org/10.1016/j.microb.2024.100124>

- O'Callaghan, M., Ballard, R. A., & Wright, D. (2022). Soil microbial inoculants for sustainable agriculture: Limitations and opportunities. *Soil Use and Management*, 38(3), 1340-1369. <https://doi.org/10.1111/sum.12811>
- Olanrewaju, O. S., & Babalola, O. O. (2019). *Streptomyces*: Implications and interactions in plant growth promotion. *Applied Microbiology and Biotechnology*, 103, 1179-1188. <https://doi.org/10.1007/s00253-018-09577-y>
- Patanè, C., Cosentino, S. L., Romano, D., & Toscano, S. (2022). Relative water content, proline, and antioxidant enzymes in leaves of long shelf-life tomatoes under drought stress and rewatering. *Plants*, 11(22), Article 3045. <https://doi.org/10.3390/plants11223045>
- Pérez-Patricio, M., Camas-Anzueto, J. L., Sanchez-Alegría, A., Aguilar-González, A., Gutiérrez-Miceli, F., & Escobar-Gómez, E. (2018). Optical method for estimating the chlorophyll contents in plant leaves. *Sensors*, 18(2), Article 650. <https://doi.org/10.3390/s18020650>
- Ragaey, M. M., Sadak, M. S., Dawood, M. F. A., Mousa, N. H. S., Hanafy, R. S., & Latef, A. A. H. A. (2022). Role of signalling molecules sodium nitroprusside and arginine in alleviating salt-induced oxidative stress in wheat. *Plants*, 11(14), Article 1786. <https://doi.org/10.3390/plants11141786>
- Renzetti, M., Funck, D., & Trovato, M. (2025). Proline and ROS: A unified mechanism in plant development and stress response? *Plants*, 14(1), Article 2. <https://doi.org/10.3390/plants14010002>
- Riahi, K., Hosni, K., Raies, A., & Oliveira, R. (2019). Unique secondary metabolites of a *Streptomyces* strain isolated from extreme salty wetland show antioxidant and antibacterial activities. *Journal of Applied Microbiology*, 127(6), 1727-1740. <https://doi.org/10.1111/jam.14428>
- Rodríguez Coca, L. I., García González, M. T., Gil Unday, Z., Jiménez Hernández, J., Rodríguez Jáuregui, M. M., & Fernández Cancio, Y. (2023). Effects of sodium salinity on rice (*Oryza sativa* L.) cultivation: A review. *Sustainability*, 15(3), Article 1804. <https://doi.org/10.3390/su15031804>
- Romano-Armada, N., Yañez-Yazlle, M. F., Irazusta, V. P., Rajal, V. B., & Moraga, N. B. (2020). Potential of bioremediation and PGP traits in *Streptomyces* as strategies for bio-reclamation of salt-affected soils for agriculture. *Pathogens*, 9(2), Article 117. <https://doi.org/10.3390/pathogens9020117>
- Sadak, M. S. (2023). Physiological role of arbuscular mycorrhizae and vitamin B1 on productivity and physio-biochemical traits of white lupine (*Lupinus termis* L.) under salt stress. *Gesunde Pflanzen*, 75, 1885-1896. <https://doi.org/10.1007/s10343-023-00855-y>
- Sadak, M. S., & Dawood, M. G. (2023). Biofertilizer role in alleviating the deleterious effects of salinity on wheat growth and productivity. *Gesunde Pflanzen*, 75, 1207-1219. <https://doi.org/10.1007/s10343-022-00783-3>
- Sadak, M. S., & Ramadan, A. A. E. (2021). Impact of melatonin and tryptophan on water stress tolerance in white lupine (*Lupinus termis* L.). *Physiology and Molecular Biology of Plants*, 27(3), 469-481. <https://doi.org/10.1007/s12298-021-00958-8>
- Sadak, M. S., Sekara, A., Al-Ashkar, I., Habib-Ur-Rahman, M., Skalicky, M., Brestic, M., Kumar, A., Sabagh, A. E., & Abdelhamid, M. T. (2022). Exogenous aspartic acid alleviates salt stress-induced decline in growth by enhancing antioxidants and compatible solutes while reducing reactive oxygen species in wheat. *Frontiers in Plant Science*, 13, Article 987641. <https://doi.org/10.3389/fpls.2022.987641>

- Santoyo, G., Guzmán-Guzmán, P., Parra-Cota, F. I., Santos-Villalobos, S. d. I., Orozco-Mosqueda, M. d. C., & Glick, B. R. (2021). Plant growth stimulation by microbial consortia. *Agronomy*, *11*(2), Article 219. <https://doi.org/10.3390/agronomy11020219>
- Sarkar, G., & Suthindhiran, K. (2022). Diversity and biotechnological potential of marine actinomycetes from India. *Indian Journal of Microbiology*, *62*(4), 475-493. <https://doi.org/10.1007/s12088-022-01024-x>
- Sarsekeyeva, F. K., Sadvakasova, A. K., Sandybayeva, S. K., Kossalbayev, B. D., Huang, Z., Zayadan, B. K., Akmukhanova, N. R., Leong, Y. K., Chang, J. S., & Allakhverdiev, S. I. (2024). Microalgae- and cyanobacteria-derived phytostimulants for mitigation of salt stress and improved agriculture. *Algal Research*, *82*, Article 103686. <https://doi.org/10.1016/j.algal.2024.103686>
- Silva, G. C., Kitano, I. T., Ribeiro, I. A. F., & Lacava, P. T. (2022). The potential use of actinomycetes as microbial inoculants and biopesticides in agriculture. *Frontiers in Soil Science*, *2*, Article 833181. <https://doi.org/10.3389/fsoil.2022.833181>
- Sultana, S., Paul, S. C., Parveen, S., Alam, S., Rahman, N., Jannat, B., Hoque, S., Rahman, M. T., & Karim, M. M. (2020). Isolation and identification of salt-tolerant plant-growth-promoting rhizobacteria and their application for rice cultivation under salt stress. *Canadian Journal of Microbiology*, *66*(2), 144-160. <https://doi.org/10.1139/cjm-2019-0323>
- Tangerina, M. M. P., Furtado, L. C., Leite, V. M. B., Bauermeister, A., Velasco-Alzate, K., Jimenez, P. C., Garrido, L. M., Padilla, G., Lopes, N. P., Costa-Lotufo, L. V., & Pena Ferreira, M. J. (2020). Metabolomic study of marine *Streptomyces* sp.: Secondary metabolites and the production of potential anticancer compounds. *PLOS ONE*, *15*(12), Article e0244385. <https://doi.org/10.1371/journal.pone.0244385>
- Ullah, I., Ullah, S., Amin, F., Al-Hawadi, J. S., Okla, M. K., & Alaraidh, I. A. (2024). Germination responses of *Lens culinaris* L. seeds to osmotic potentials at cardinal temperatures using hydrothermal time model. *BMC Plant Biology*, *24*, Article 502. <https://doi.org/10.1186/s12870-024-05223-0>
- Xiong, Y. W., Gong, Y., Li, X. W., Chen, P., Ju, X. Y., Zhang, C. M., Yuan, B., Lv, Z. P., Xing, K., & Qin, S. (2019). Enhancement of growth and salt tolerance of tomato seedlings by a natural halotolerant actinobacterium *Glutamicibacter halophytocola* KLBMP 5180 isolated from a coastal halophyte. *Plant and Soil*, *445*, 307-322. <https://doi.org/10.1007/s11104-019-04310-8>
- Xu, B. L., Wang, Y. Y., & Dong, C. M. (2023). Study on marine actinomycetes and analysis of their secondary metabolites. *Life Research*, *6*(4), Article 18. <https://doi.org/10.53388/LR20230018>
- Yu, D., Boughton, B. A., Hill, C. B., Feussner, I., Roessner, U., & Rupasinghe, T. W. T. (2020). Insights into oxidised lipid modification in barley roots as an adaptation mechanism to salinity stress. *Frontiers in Plant Science*, *11*, Article 1. <https://doi.org/10.3389/fpls.2020.00001>
- Zhang, Y., Xu, J., Li, R., Ge, Y., Li, Y., & Li, R. (2023). Plants' response to abiotic stress: Mechanisms and strategies. *International Journal of Molecular Sciences*, *24*(13), Article 10915. <https://doi.org/10.3390/ijms241310915>

