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Article

Gypsum Improving Soil Properties and Microbial Communities under Seawater Irrigation in Coastal Saline Soil

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Abstract: Coastal saline soils severely limit agricultural productivity due to high salinity, elevated pH, low organic matter, and scarce freshwater resources. To evaluate seawater irrigation and gypsum amendment effects, a field experiment was conducted with varying gypsum dosages under seawater irrigation, focusing on rice growth and soil properties. The results revealed that gypsum application significantly enhanced rice grain yield by improving key yield components, while seawater irrigation alone reduced them. Gypsum also effectively lowered soil electrical conductivity (EC_e) and available potassium (AK), while markedly increasing organic carbon (OC), alkali-hydrolysable nitrogen (AN), Olsen phosphorus (OP), bacterial diversity (bactH), fungal diversity (fungH), and total phospholipid fatty acids (PLFA). Seawater irrigation alone obviously elevated soil pH, EC_e, and AK but significantly decreased OC, AN, OP, bactH, fungH, and total PLFA, though it increased fungal PLFA (fungPLFA). Combining gypsum with seawater irrigation noticeably reduced soil pH, EC_e, OC, AN, OP, bactH, fungH, and total PLFA, while markedly increasing AK, the fungPLFA to bacterial PLFA ratio (F/B), and the Gram-positive to Gram-negative bactPLFA ratio (G^+/G^-). Regression analysis indicated soil pH drove bactH, fungH, total PLFA, bactPLFA, fungPLFA, and G^+ bactPLFA, whereas soil salinity dominated G^- bactPLFA, F/B, and G^+/G^- under gypsum-seawater irrigation. This study concluded that soil pH and salinity jointly govern microbial community structure, while gypsum improves soil chemical properties and microbial diversity. These findings provide valuable insights for optimizing gypsum and seawater irrigation strategies to remodel microbial communities and enhance soil fertility, thus promoting sustainable agriculture in coastal saline regions.

Keywords: pH; electrical conductivity; soil nutrient; microbial diversity; microbial biomass; phospholipid fatty acid

1. Introduction

Coastal saline soils are typically characterized by elevated salinity and pH levels, low organic matter content, and limited freshwater availability in coastal regions. High soil salinity and pH not only significantly alter soil physicochemical properties and biological characteristics but also adversely affect plant growth [1,2]. Additionally, freshwater scarcity in coastal areas restricts the application of traditional leaching techniques for saline soil remediation [3]. During the growing season, insufficient rainfall and freshwater shortages often compel farmers to adopt seawater irrigation for crop cultivation. To mitigate salt accumulation in the soil, amendments such as gypsum ($CaSO_4 \cdot 2H_2O$) are recommended. Gypsum supplies Ca^{2+} ions to displace exchangeable Na^+, thereby facilitating the leaching of excess soluble salts through irrigation for reducing soil salinity and pH [4]. While seawater irrigation and gypsum amendments have been extensively studied for their effects on crop growth, their combined impact on soil microbial communities remains largely unexplored [5,6]. Understanding how soil salinity and pH influence microbial communities is critical for assessing soil ecological functions and developing effective strategies to enhance fertility in saline soils [7].

Numerous studies have demonstrated that irrigation with diluted seawater can enhance both crop yield and quality [6,8]. Previous research indicated that seawater with a salinity below 5 $g \cdot L^{-1}$ was suitable for irrigating crops such as barley, wheat, corn, cotton, and sunflowers without causing significant soil salinization, provided that rainfall leaching occurs at reasonable levels [8–13]. However, continuous seawater irrigation may lead to salt accumulation and soil salinization during the evaporation of surface soil moisture, adversely affecting soil-crop systems [6,10,14–21]. Long-term excessive use of seawater can further exacerbate salt accumulation in soil, with sodium ions increasing not only soil salinity [8,20,22] and pH [6] but also water-soluble nitrogen content [23], soil carbon storage, and mineralization rates [24]. Additionally, sodium presence disrupted soil microbial biomass [23], reduced microbial diversity [25–27], and altered community structure [28] and composition [14,16,21]. These findings suggest that seawater irrigation can indirectly alter soil nutrient availability by affecting microbial communities. Contrary to these concerns, some studies indicated that seawater irrigation, due to its slightly acidic pH and low salinity, had minimal impact on soil microbial biomass when seasonal heavy rainfall effectively leached excess salts [6,23]. Despite extensive research on the physical, chemical, and biological effects of seawater irrigation on soils, the mechanisms and factors governing soil microbial community dynamics remain unresolved and contentious.

Gypsum application has been widely recognized as an effective agricultural practice to mitigate the adverse effects of seawater irrigation on soils [2,3,14,29–31]. This efficacy stemmed from gypsum's ability to enhance Ca^{2+} activity through the dissolution of calcium carbonate ($CaCO_3$) [32]. Additionally, calcium sulfate ($CaSO_4$) reacted rapidly with sodium salts (e.g., NaCl, Na_2CO_3, and $NaHCO_3$) in seawater irrigation, forming sodium sulfate (Na_2SO_4), which could be efficiently leached from the soil [33,34]. A common practice for improving soil sodicity involved surface application of 5–10 $Mg \cdot hm^{-2}$ gypsum every 3–5 years [35]. For complete neutralization of sodicity, however, 22.7 $Mg \cdot hm^{-2}$ gypsum was required [36]. Research corroborated that gypsum could ameliorate saline soils in arid and semiarid regions by replacing exchangeable Na^+ with Ca^{2+} [37], facilitating the transport of excess Na^+ from surface to deeper soil layers [38], reducing soil salinity and pH [3,37,39], enhancing soil physical properties in seawater irrigation systems [40], increasing organic carbon (OC) content [38], and promoting soil microbial biomass, fungi, bacteria, Gram-positive (G^+) bacteria, and Gram-negative (G^-) bacteria [41]. However, some studies indicated that gypsum addition may not significantly affect soil microbial biomass under long-term seawater irrigation [42,43]. While most research has focused on gypsum's role in improving arid and semiarid soils, its application in coastal saline soil remains significantly understudied. Moreover, the mechanistic linkages between gypsum addition and soil microbial community dynamics—particularly in the context of combined gypsum and seawater irrigation—have not been well documented or understood in coastal saline environments.

To mitigate the harmful effects of seawater irrigation and enhance gypsum's ability to leach soluble salts from root zones in coastal saline soils, simultaneous application of gypsum and seawater irrigation is essential [4]. The present study aims to evaluate the impacts of seawater irrigation, gypsum application, and their combined use on soil microbial communities in coastal saline soils using denaturing gradient gel electrophoresis (DGGE) fingerprinting and phospholipid fatty acid (PLFA) profile analysis. We hypothesized that seawater irrigation would negatively affect soil chemical properties and microbial communities. Specifically, we anticipated that soil salinity would independently or interact with soil pH to shape microbial communities, as both factors were critical regulators of soil microbial diversity [44–46]. Additionally, we proposed that gypsum would improve soil pH, salinity, and nutrient availability, thereby altering soil microorganisms. This hypothesis was supported by evidence that gypsum was negatively correlated with soil pH and salinity [24,31,39,47–50]. More specifically, we expected gypsum to increase soil nutrients, enhance microbial biomass, and modify microbial community structure. Finally, we hypothesized that the combined use of gypsum and seawater irrigation would significantly regulate soil chemical properties and microbial communities. Here, we anticipated that soil salinity would exert a stronger influence than pH on microbial community composition, as salinity was the primary environmental determinant of microbial communities across diverse ecosystems worldwide, outweighing the effects of pH and other physicochemical factors [51].

2. Materials and Methods

2.1. Experimental Site Description

The experimental site was situated in Cixi City, Zhejiang Province, China (latitude 121°12′ N, longitude 30°21′ E). The soil at this location originated from modern marine and fluvial deposits in Hangzhou Bay and was classified as coastal solonchak. Its composition included 7.4% sand, 7.7% clay, and 84.9% silt. The soil exhibited a pH of 8.2, an electrical conductivity of saturated paste extracts (EC_e) of 6.2 $dS \cdot m^{-1}$, and contained 5.06 $g \cdot kg^{-1}$ OC, 1.88 $g \cdot kg^{-1}$ salt content, 30.8 $mg \cdot kg^{-1}$ alkali-hydrolyzable nitrogen (AN), 3.5 $mg \cdot kg^{-1}$ Olsen phosphorus (OP), and 407.9 $mg \cdot kg^{-1}$ available potassium (AK). The site's climate falls within the subtropical monsoon zone, characterized by an average annual temperature of 16.3 °C and an average annual precipitation of 1325 mm.

2.2. Experimental Design

2.2.1. Experimental Treatment

The experiment was conducted with twelve treatments and three replicates, arranged in a randomized block design. These treatments involved three different gypsum application rates (0, 5, and 10 $Mg \cdot hm^{-2}$) and four levels of irrigation water salinity (0, 1.5, 2.5, and 3.5 $g \cdot L^{-1}$). The twelve treatment combinations were as follows: (i) Untreated soils irrigated with freshwater (G_0S_0); (ii) Soils treated with 5 $Mg \cdot hm^{-2}$ gypsum and irrigated with freshwater (G_5S_0); (iii) Soils treated with 10 $Mg \cdot hm^{-2}$ gypsum and irrigated with freshwater ($G_{10}S_0$); (iv) Untreated soils irrigated with water of 1.5 $g \cdot L^{-1}$ salinity ($G_0S_{1.5}$); (v) Soils treated with 5 $Mg \cdot hm^{-2}$ gypsum and irrigated with water of 1.5 $g \cdot L^{-1}$ salinity ($G_5S_{1.5}$); (vi) Soils treated with 10 $Mg \cdot hm^{-2}$ gypsum and irrigated with water of 1.5 $g \cdot L^{-1}$ salinity ($G_{10}S_{1.5}$); (vii) Untreated soils irrigated with water of 2.5 $g \cdot L^{-1}$ salinity ($G_0S_{2.5}$); (viii) Soils treated with 5 $Mg \cdot hm^{-2}$ gypsum and irrigated with water of 2.5 $g \cdot L^{-1}$ salinity ($G_5S_{2.5}$); (ix) Soils treated with 10 $Mg \cdot hm^{-2}$ gypsum and irrigated with water of 2.5 $g \cdot L^{-1}$ salinity ($G_{10}S_{2.5}$); (x) Untreated soils irrigated with water of 3.5 $g \cdot L^{-1}$ salinity ($G_0S_{3.5}$); (xi) Soils treated with 5 $Mg \cdot hm^{-2}$ gypsum and irrigated with water of 3.5 $g \cdot L^{-1}$ salinity ($G_5S_{3.5}$); (xii) Soils treated with 10 $Mg \cdot hm^{-2}$ gypsum and irrigated with water of 3.5 $g \cdot L^{-1}$ salinity ($G_{10}S_{3.5}$). The gypsum application rates were selected based on recommendations from previous studies [35,36], while the irrigation water salinity levels were chosen after comprehensive consideration of prior research [9–11].

2.2.2. Irrigation Water Preparation

The irrigation water was prepared by mixing freshwater from rainwater tanks with natural seawater collected from ditches. A customized proportional controller, equipped with a variable frequency pump, was used to blend these two water sources. This system enabled time-based automatic pulse irrigation and provided real-time, accurate monitoring of the irrigation water's salinity level. The freshwater had a pH of 7.0 and no detectable salinity. The natural seawater exhibited a pH of 8.57, an electrical conductivity (EC) of 35.0 $dS \cdot m^{-1}$ (equivalent to a salinity of 21.22 $g \cdot L^{-1}$), and contained the following ions: Na^+ 7.29 $g \cdot L^{-1}$, Mg^{2+} 0.92 $g \cdot L^{-1}$, Ca^{2+} 0.27 $g \cdot L^{-1}$, K^+ 0.27 $g \cdot L^{-1}$, and Cl^- 14.64 $g \cdot L^{-1}$.

2.2.3. Gypsum Application

Gypsum ($CaSO_4 \cdot 2H_2O$, 98% purity, with particle size <0.3 mm in diameter) was used as a soil amendment. Its properties included a pH of 7.12, an EC of 2.23 $dS \cdot m^{-1}$, and the following elemental composition: Ca 229.6 $g \cdot kg^{-1}$, Mg 2.4 $g \cdot kg^{-1}$, S 216.9 $g \cdot kg^{-1}$, and Al 1.0 $g \cdot kg^{-1}$. Gypsum was mixed into the 0–20 cm soil layer before irrigation.

2.2.4. Rice Cultivation

After preparing the soil-gypsum mixture, rice seedlings were transplanted into the plots. The rice variety used was 'Yongyou 1450'. Base fertilizer consisted of compound fertilizer (N: P_2O_5: K_2O = 15:15:15) applied at 750 $kg \cdot hm^{-2}$, supplemented with urea topdressing at 180 $kg \cdot hm^{-2}$. Each plot measured 5 m × 5 m in size. During the rice growth period, each plot received a total irrigation volume of 7700 $m^3 \cdot hm^{-2}$, delivered in seven equal applications (each application: 110 mm). The irrigation interval was adjusted based on soil moisture content and rice growth stage requirements. All other necessary agronomic practices (e.g., pest control, weed management) were uniformly applied across all plots. Rice was harvested on day 153 after transplanting.

2.3. Data Collection and Measurements

2.3.1. Soil Sampling and Physicochemical Analysis

Soil Sampling and Preparation: On the day following rice harvesting, bulk soil samples were collected from the 0–20 cm depth layer. For each experimental plot, one composite soil sample was assembled by combining ten randomly collected cores (each with a diameter of 1.5 cm). After removing visible stones and plant residues, each fresh soil sample was divided into two equal portions and thoroughly mixed. One portion was immediately frozen at −20 °C and subsequently freeze-dried for community deoxyribonucleic acid (DNA) extraction and PLFA analysis. The other portion was air-dried and passed through a 2 mm sieve for physicochemical analysis.

Physicochemical Analysis: Soil texture was determined using the hydrometer method. Soil pH was measured at a soil-to-water ratio of 1:5 after shaking at 28 °C for 30 min. Soil electrical conductivity ($EC_{1:5}$) was measured at 25 °C using a soil-to-water ratio of 1:5 after 1 h of end-to-end oscillation [52]. The $EC_{1:5}$ values were converted to EC_e using the equation: $EC_e = 0.414 + 8.450 \times EC1{:}5$ [53]. Soil OC was quantified using the dichromate oxidation method. AN was determined via the diffusion absorption method. OP was measured using the Olsen method. AK was assessed using the ammonium acetate extract-flame photometric method [54].

2.3.2. DNA Extraction and DGGE

Community DNA Extraction and Polymerase Chain Reaction (PCR) Amplification: Community DNA extraction and purification were performed using the soil DNA kit (Omega, D5625-01, USA) following the manufacturer's protocol. Bacterial 16S rDNA was amplified with the universal primer pair 357F and 518R. To facilitate separation of PCR fragments in DGGE gels, a GC clamp was attached to the 5'-end of the forward primer. For fungal 18S rDNA amplification, nested PCR was conducted using the primer pairs ITS1F/ITS4 and ITS1FGC/ITS2. All PCR reactions were carried out using a Thermal Cycler (Eppendorf, Hamburg, Germany) [55].

DGGE Analysis: The amplified products were analyzed by DGGE on a 10% polyacrylamide gel using the Bio-Rad D-Code System (Bio-Rad Laboratories, Hercules, CA, USA). For bacterial community analysis, the gel contained a denaturant gradient of 40% to 60% in a 1× Tris-acetate-EDTA buffer at 60 °C, and electrophoresis was performed at 110 V for 10 h. For fungal community analysis, the gel contained a denaturant gradient of 20% to 40% under the same buffer conditions, and electrophoresis was conducted at 150 V for 6 h [52].

Diversity Calculation: Bacterial diversity (bactH) and fungal diversity (fungH) were quantified using the Shannon index (H) to assess changes in diversity across all treatments. The Shannon index was calculated with the following equation [52]: $H = -(ni/N)\ \ln(ni/N)$.

Where ni is the ith band intensity and N is the total intensity of all bands in a lane sample of DGGE banding patterns.

2.3.3. PLFA Analysis

PLFA Extraction and Analysis: Soil phospholipid extraction and PLFA analysis were conducted following the method described by Williams (2007) [56]. Briefly, 4 g of freeze-dried soil samples were extracted overnight in a mixture of chloroform, methanol, and 50 mM phosphate buffer (pH 7.1). The PLFA fraction was subsequently separated using a solid-phase silica gel column (Supelco, Inc., Bellefonte, PA, USA) with sequential elusion using chloroform, acetone, and methanol. Prior to methylation, fatty acid 19:0 was added as an internal standard. The recovered phospholipid fraction was saponified to yield fatty acid methyl esters (FAMEs), which were analyzed using the MIDI Sherlock Microbial Identification System (MIDI Inc., Newark, NJ, USA) coupled with an Agilent 7890 gas chromatograph equipped with a flame ionization detector.

Microbial Biomass Estimation: Total microbial biomass was estimated based on the total concentration of PLFAs (totPLFA) [57]. Gram-positive bacterial biomass (G^+ bactPLFA) was quantified as the sum of the following PLFAs: i14:0, i15:0, a15:0, i16:0, a17:0, and i17:0 [58]. Gram-negative bacterial biomass (G^- bactPLFA) was assessed using the sum of PLFAs 16:1ω5c, 16:1ω7c, cy17:0, 17:1ω8c, 18:1ω7c, 18:1ω9c, and cy19:0 [59,60]. Bacterial biomass (bactPLFA) was represented by the sum of G^+ bactPLFA, G^- bactPLFA, and normal saturated fatty acids 14:0, 15:0, 16:0, 17:0, and 18:0 [60]. Fungal biomass (fungPLFA) was estimated to be using the PLFA 18:2ω6,9c [61].

2.4. Data Analysis

All data were processed using Microsoft Excel 2019 and analyzed with SPSS 20.0. Significant differences in yield and soil chemical and microbial parameters among treatments were assessed using two-way analysis of variance (ANOVA), followed by Tukey's honestly significant difference (HSD) test for post hoc comparisons at a significance level of $p < 0.05$ (GenStat for Windows 8.0, VSN International Ltd., Redditch, UK, 2005).

Linear regression analysis was performed using SPSS Statistical Software 16.0 to evaluate relationships between microbial parameters and abiotic factors. Additionally, stepwise linear regression analysis was employed to quantify associations between microbial parameters and PLFAs. The stepping criteria for variable entry and removal were based on the significance level of the F-value, set at $p < 0.05$, ensuring that all variables included in the final equation were statistically significant.

3. Results

3.1. Yield

The reproductive growth of rice was visibly influenced by gypsum application and salinity levels (Table 1). For instance, treatment $G_{10}S_0$ achieved the highest grain yield (10,140.6 kg·ha^{-1}), which was statistically significantly higher ($p \leq 0.05$) than yields from all other treatments. Conversely, treatment $G_0S_{3.5}$ yielded the lowest grain production (3213.6 kg·ha^{-1}), which was statistically significantly lower ($p \leq 0.05$) compared to all other treatments. Furthermore, gypsum application significantly enhanced rice grain yields at the same level of irrigation water salinity. The yield components responsible for these differences included the number of panicles per unit area, grains per panicle, the proportion of filled grains, and the thousand-grain weight. Seawater irrigation reduced these yield components, whereas increasing gypsum application rates markedly improved them. Notably, no statistically significant differences were observed in rice grain dry matter weight (%) across treatments.

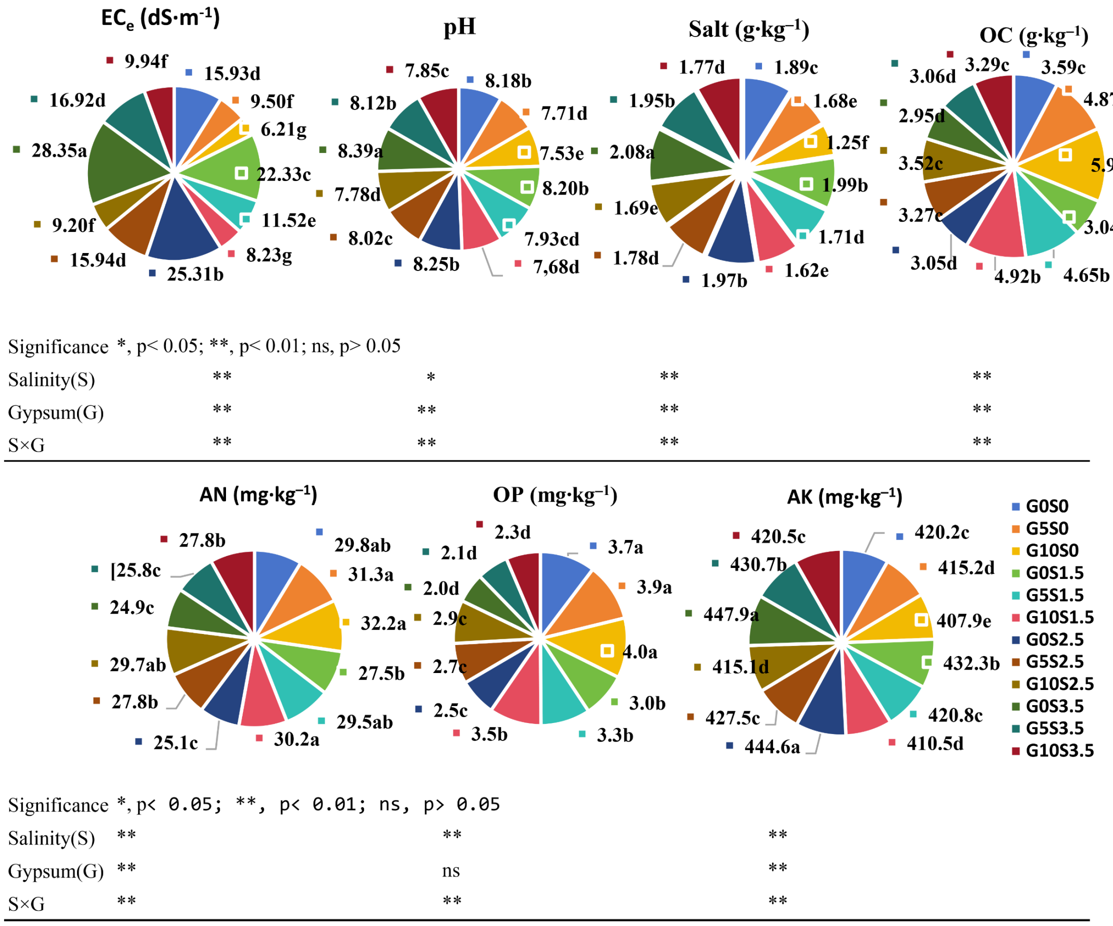
Table 1. Yield components in rice plants subjected to different treatments with gypsum and salinity in the saline soil in Cixi City, Zhejiang Province, China.

Treatment	Panicles/m^2 (no.)	Grains/Panicle (no.)	Thousand-Grain Weight (g)	Filled Grain (%)	Grain Dry Matter (%)	Yield (kg·ha^{-1})
G_0S_0	273.7 b	141.6 b	25.15 b	91.88 ab	83.80 a	6006.9 c
G_5S_0	280.0 ab	140.6 b	28.80 ab	94.85 a	83.33 a	7172.7 b
$G_{10}S_0$	298.0 a	171.9 a	31.02 a	96.06 a	83.00 a	10140.6 a
$G_0S_{1.5}$	270.0 b	130.1 b	23.37 c	93.99 ab	82.45 a	5091.9 cd
$G_5S_{1.5}$	280.0 ab	127.2 b	25.63 b	90.66 ab	83.43 a	5526.4 c
$G_{10}S_{1.5}$	281.8 ab	156.7 ab	27.42 ab	93.68 ab	82.91 a	7527.3 b
$G_0S_{2.5}$	268.4 bc	129.1 b	21.15 cd	86.31 b	82.26 a	4164.6 d
$G_5S_{2.5}$	272.5 b	147.7 b	23.92 c	90.53 ab	82.81 a	5776.8 c
$G_{10}S_{2.5}$	275.0 b	140.6 b	23.80 c	90.85 ab	83.33 a	5576.1 c
$G_0S_{3.5}$	238.9 d	120.5 c	20.97 d	80.52 c	82.60 a	3213.6 e
$G_5S_{3.5}$	249.7 c	126.2 b	22.65 c	87.99 b	81.95 a	4119.4 d
$G_{10}S_{3.5}$	251.3 c	134.3 b	23.23 c	88.85 b	84.57 a	4715.2 d

Means followed by different letters in each column indicate significant differences according to Tukey's test ($p \leq 0.05$).

3.2. Soil Chemical Characteristics

Seawater irrigation significantly increased soil pH, EC_e, salt content, and AK while decreasing OC, AN, and OP as irrigation water salinity rose (Figure 1). Conversely, gypsum markedly reduced soil pH, EC_e, salt content, and AK, while increasing OC and AN with the increase of gypsum dosage. No significant differences were observed in OP content across treatments in the coastal saline soil. Furthermore, the combined use of gypsum and seawater irrigation distinctly influenced soil properties, including pH, EC_e, salt content, OC, AN, OP, and AK. Increasing the gypsum dosage notably decreased pH, EC_e, salt content, and AK while strongly boosting OC and AN at the same level of irrigation water salinity. Meanwhile, seawater irrigation alone significantly reduced OP content as irrigation water salinity increased.



Significance *, p< 0.05; **, p< 0.01; ns, p> 0.05	ECe	pH	Salt	OC
Salinity(S)	**	*	**	**
Gypsum(G)	**	**	**	**
S×G	**	**	**	**

Significance *, p< 0.05; **, p< 0.01; ns, p> 0.05	AN	OP	AK
Salinity(S)	**	**	**
Gypsum(G)	**	ns	**
S×G	**	**	**

Figure 1. Soil chemical properties in the coastal saline soil with gypsum application and seawater irrigation. The different lowercase letters after the numbers indicate differences between treatments at the 0.05 level (n = 3).

3.3. Microbial Genetic Diversity, Biomass and Community Structure

Significant changes in microbial genetic diversity were observed with gypsum application and seawater irrigation (Figure 2 and Table 2). Both bactH and fungH decreased as irrigation water salinity increased, while they significantly increased with higher gypsum application rates. The combined use of gypsum and seawater irrigation further reduced bactH and fungH compared to treatments where gypsum was applied with freshwater irrigation, but it still resulted in higher values than those observed in treatments without gypsum.

The effects of gypsum application and seawater irrigation on microbial biomass were also evident (Figure 3 and Table 2). Seawater irrigation with increasing salinity significantly reduced totPLFA, bactPLFA, and G^{-} bactPLFA, while it increased fungPLFA, F/B, and G^{+}/G^{-}. In contrast, totPLFA, bactPLFA, fungPLFA, G^{+} bactPLFA, G^{-} bactPLFA, F/B, and G^{+}/G^{-} significantly increased as gypsum dosage rose. Additionally, the combined use of gypsum and seawater irrigation markedly reduced totPLFA, bactPLFA, and G^{-} bactPLFA compared to gypsum-freshwater irrigation treatments, while greatly enhancing fungPLFA, G^{+} bactPLFA, F/B, and G^{+}/G^{-} compared to treatments without gypsum.

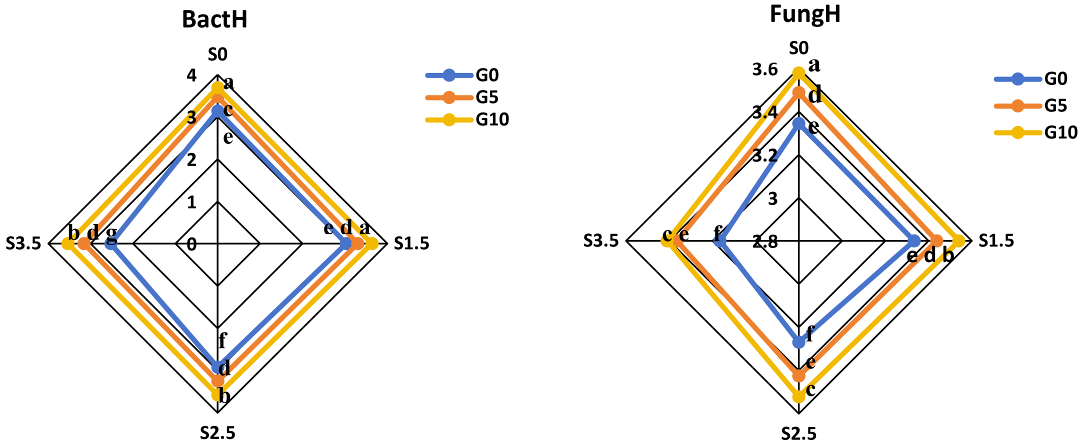


Figure 2. The bacterial (bactH) and fungal (fungH) genetic diversity indices with gypsum application and seawater irrigation. The different lowercase letters are significant differences between treatments at the 0.05 level (n = 3).

Table 2. F-values from two-way analysis of variance of the effects of gypsum application and seawater irrigation on microbial parameters (** $p < 0.01$).

Parameters	Gypsum (G)	Salinity (S)	G × S	Parameters	Gypsum (G)	Salinity (S)	G×S
bactH	2047.09 **	277.39 **	50.22 **	i16:0	75.50 **	15.35 **	24.30 **
fungH	900.55 **	110.13 **	12.54 **	16:1ω5c	119.53 **	321.43 **	1.86
totPLFA	9826.42 **	1700.20 **	85.12 **	16:1ω7c	26.63 **	82.01 **	2.31
bactPLFA	131.18 **	52.46 **	5.94 **	17:0	352.71 **	255.59 **	31.63 **
fungPLFA	373.53 **	23.98 **	2.09	i17:0	188.38 **	22.29 **	20.51 **
G^+ bactPLFA	186.88 **	3.33	8.97 **	a17:0	3.29	77.23 **	1.74
G^- bactPLFA	58.73 **	126.31 **	7.81 **	cy17:0	33.64 **	260.77 **	2.20
F/B	260.55 **	148.01 **	4.20 **	17:1ω8c	32.25 **	294.88 **	2.49
G^+/G^-	29.96 **	196.20 **	8.95 **	18:1ω7c	29.13 **	112.31 **	5.08 **
i14:0	248.64 **	361.81 **	24.50 **	18:1ω9c	88.00 **	81.43 **	2.54
i15:0	86.07 **	59.28 **	5.45 **	18:2ω6,9c	373.53 **	23.98 **	2.09
a15:0	179.35 **	225.55 **	21.80 **	cy19:0	197.61 **	119.13 **	8.49 **

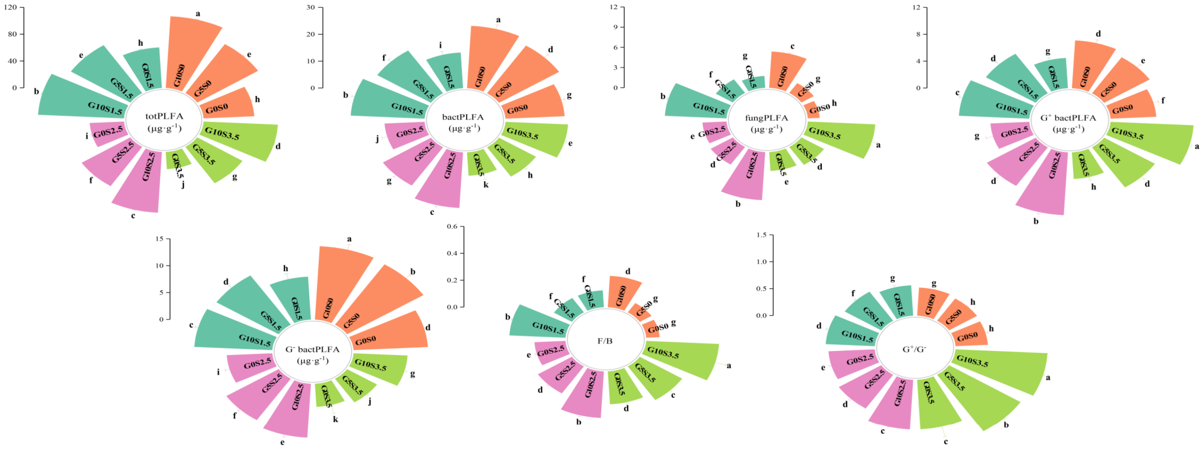


Figure 3. Total concentration of phospholipid fatty acids (totPLFA), bacterial PLFA (bactPLFA), fungal PLFA (fungPLFA), G^+ bacterial PLFA (G^+ bactPLFA), G^- bacterial PLFA (G^- bactPLFA), fungPLFA/bactPLFA (F/B) and G^+ bactPLFA/G^- bactPLFA (G^+/G^-) of the microbial communities with conjunctive use of gypsum and seawater irrigation. The different lowercase letters are significant differences between treatments at the 0.05 level. Error bars indicate standardized deviation (n = 3).

3.4. Microbial PLFA Composition

Seawater irrigation significantly increased the concentrations of specific PLFAs (e.g., i15:0, a15:0, i16:0, and 18:2ω6,9c) compared to freshwater irrigation (Figure 4 and Table 2). Conversely, the concentrations of other PLFAs (e.g., i14:0, 16:1ω5c, 16:1ω7c, 17:0, i17:0, a17:0, cy17:0, 17:1ω8c, 18:1ω7c, 18:1ω9c, and cy19:0) significantly decreased as irrigation water salinity rose. By contrast, increasing gypsum dosage markedly increased the concentrations of i14:0, i15:0, a15:0, i16:0, 17:0, i17:0, a17:0, cy17:0, 17:1ω8c, 18:1ω9c, cy19:0, and 18:2ω6,9c, while notably reducing the concentrations of 16:1ω5c, 16:1ω7c, and 18:1ω7c. Additionally, the combined use of gypsum and seawater irrigation significantly reduced the concentrations of i14:0, 17:0, i17:0, 18:1ω7c, and cy19:0 compared to freshwater irrigation treatments, while effectively increasing the concentrations of i15:0, a15:0, and i16:0. However, no additive effects of gypsum and seawater irrigation were observed on the concentrations of 16:1ω5c, 16:1ω7c, a17:0, cy17:0, 17:1ω8c, 18:1ω9c, or 18:2ω6,9c.

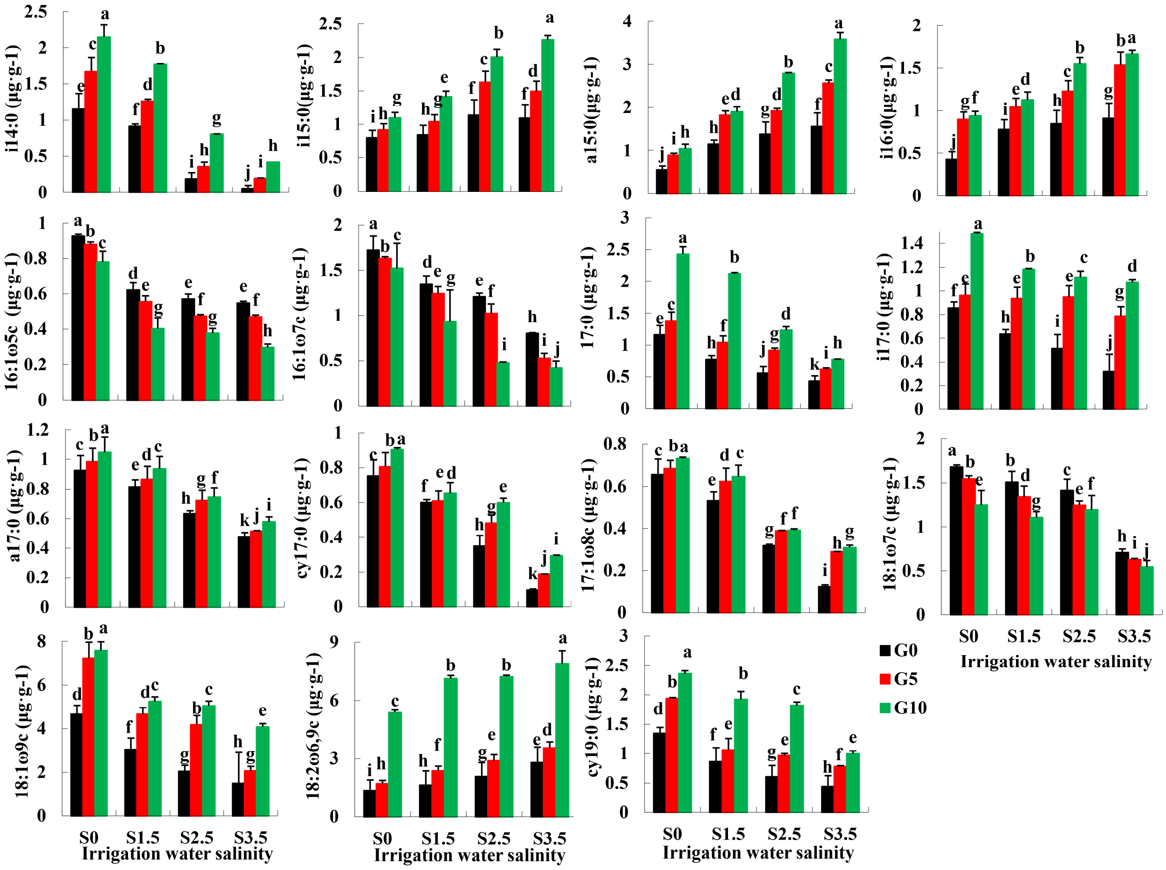


Figure 4. The concentration of phospholipid fatty acids i14:0, 16:1ω5c, 16:1ω7c, 17:0, a17:0, cy17:0, 17:1 ω8C, 18:1ω7c, 18:1ω9c, i15:0, a15:0, i16:0, i17:0, cy19:0 and 18:2ω6, 9C of the microbial communities with conjunctive use of gypsum and seawater irrigation. The different lowercase letters are significant differences between treatments at the 0.05 level. Error bars indicate standardized deviation (n = 3).

3.4. Correlations of the Microbial Parameters to pH and Salinity

Linear regression analysis revealed significant negative correlations between soil pH and several microbial and fatty acid parameters (Table 3). Specifically, soil pH was negatively correlated with bactH, fungH, totPLFA, bactPLFA, G^+ bactPLFA, G^-bactPLFA, fungPLFA, F/B, G^+/G^-, and specific fatty acids (e.g., i14:0, i15:0, a15:0, i16:0, 17:0, i17:0, a17:0, cy17:0, 17:1ω8c, 18:1ω9c, 18:2ω6,9c, and cy19:0). Conversely, soil pH exhibited marked positive correlations with 16:1ω5c, 16:1ω7c, and 18:1ω7c. Similarly, soil EC_e showed significant negative relationships with bactH, fungH, totPLFA, bactPLFA, G^- bactPLFA, i14:0, 16:1ω5c, 16:1ω7c, 17:0, a17:0, cy17:0, 17:1ω8c, 18:1ω7c, and 18:1ω9c, while it had significant positive relationships with fungPLFA, F/B, G^+/G^-, i15:0, a15:0, i16:0, and 18:2ω6,9c. No significant relationships were observed between EC_e and G^+ bactPLFA, i17:0, or cy19:0.

Table 3. Linear regression analysis results related to the microbial parameters with soil pH and salinity (EC_e) ($Y = b_0 + b_1 \times pH + b_2 \times EC_e$, n = 36; β, standardized regression coefficient; * $p < 0.05$; ** $p < 0.01$).

Parameters (Y)	b_0	pH		EC_e		R^2	F
		b_1	β	b_2	β		
bactH	10.717	−0.885	−0.881 **	−0.021	−0.392 **	0.930	220.112 **
fungH	6.142	−0.325	−0.895 **	−0.007	−0.381 **	0.946	287.356 **
totPLFA	608.300	−63.226	−0.877 **	−1.684	−0.442 **	0.965	455.058 **
bactPLFA	106.118	−10.302	−0.757 **	−0.416	−0.578 **	0.906	159.616 **
fungPLFA	51.249	−6.017	−0.848 **	0.100	0.267 **	0.791	62.484 **
G$^+$ bactPLFA	46.913	−5.036	−0.898 **	0.040	0.136	0.825	77.762 **
G$^-$ bactPLFA	48.112	−4.14	−0.462 **	−0.393	−0.829 **	0.901	149.376 **
F/B	1.589	−0.187	−0.565 **	0.012	0.656 **	0.749	49.360 **
G$^+$/G$^-$	2.181	−0.241	−0.278 **	0.040	0.881 **	0.853	95.448 **
i14:0	11.444	−1.165	−0.531 **	−0.087	−0.749 **	0.843	88.528 **
i15:0	8.086	−0.906	−0.647 **	0.042	0.565 **	0.739	46.695 **
a15:0	11.819	−1.406	−0.545 **	0.099	0.727 **	0.825	77.979 **
i16:0	6.344	−0.682	−0.620 **	0.019	0.333 *	0.495	16.176 **
16:1ω5c	−1.180	0.253	0.433 **	−0.022	−0.709 **	0.691	36.839 **
16:1ω7c	−2.489	0.539	0.394 *	−0.060	−0.828 **	0.841	87.290 **
17:0	11.166	−1.134	−0.628 **	−0.064	−0.666 **	0.837	84.881 **
i17:0	7.375	−0.791	−0.842 **	−0.005	−0.100	0.720	42.338 **
a17:0	1.846	−0.086	−0.147 *	−0.028	−0.921 **	0.870	110.284 **
cy17:0	2.682	−0.205	−0.275 **	−0.037	−0.928 **	0.937	244.120 **
17:1ω8c	2.001	−0.141	−0.242 **	−0.029	−0.939 **	0.940	256.244 **
18:1ω7c	−1.399	0.381	0.360 *	−0.035	−0.633 **	0.531	18.666 **
18:1ω9c	36.612	−3.658	−0.607 **	−0.207	−0.648 **	0.788	61.441 **
18:2ω6,9c	51.249	−6.017	−0.848 **	0.100	0.267 **	0.791	62.484 **
cy19:0	11.884	−1.310	−0.689 **	−0.003	0.033	0.476	15.014 **

In linear regression analysis, the variable with the highest determination coefficient (|β|) is considered the most influential independent variable [62]. As shown in Figure 5, soil pH had a greater impact than EC_e on bactH, fungH, totPLFA, bactPLFA, fungPLFA, G$^+$ bactPLFA, i15:0, i16:0, i17:0, 18:2ω6,9c, and cy19:0, as indicated by its larger determination coefficients. However, soil pH contributed less than EC_e to G$^-$ bactPLFA, F/B, G$^+$/G$^-$, i14:0, a15:0, 16:1ω5c, 16:1ω7c, 17:0, a17:0, cy17:0, 17:1ω8c, 18:1ω7c, and 18:1ω9c due to its smaller determination coefficients.

Stepwise linear regression analysis (Table 4) identified two PLFAs (17:0 and i17:0) as significant contributors to bactH, with i17:0 having a greater contribution due to its higher determination coefficient. Additionally, i15:0, i16:0, 16:1ω5c, 17:0, and 18:1ω9c significantly contributed to totPLFA, with 18:1ω9c exhibiting the strongest influence (determination coefficient = 0.663). Similarly, 18:1ω9c had the largest contribution to bactPLFA and G$^-$ bactPLFA, while a15:0 dominated in G$^+$ bactPLFA and G$^+$/G$^-$. Moreover, 18:2ω6,9c significantly contributed to fungH and fungPLFA and was the primary driver of F/B.

Table 4. Stepwise linear regression analysis results related to the microbial parameters (Y) with the PLFAs (X_i) ($Y = b_0 + b_1X_1 \ldots + b_iX_i$, n = 36; β, standardized regression coefficient; * $p < 0.05$; ** $p < 0.01$).

Parameters (Y)	b_0	PLFAs (X_i)	b_i	β	R^2	F
Bact H	2.366	17:0	0.239	0.431 **	0.901	150.330 **
		i17:0	0.707	0.661 **		
Fung H	3.289	18:2ω6,9c	0.033	0.637 **	0.406	23.204 **
Total PLFA	62.409	i15:0	−27.859	−0.541 **	0.946	106.076 **
		i16:0	34.040	0.520 **		
		16:1ω5c	−67.274	−0.545 **		
		17:0	14.495	0.364 **		
		18:1ω9c	7.922	0.663 **		
BactPLFA	2.357	i14:0	0.937	0.151 **	0.995	1020.390 **
		i15:0	2.870	0.295 **		
		i17:0	1.538	0.106 **		
		17:1ω8c	8.633	0.368 **		
		18:1ω9c	0.933	0.413 **		
		cy19:0	0.631	0.088 **		
FungPLFA	0	18:2ω6,9c	1	1 **	1	0.000 **

Table 4. *Cont.*

Parameters (Y)	b_0	PLFAs (X_i)	b_i	β	R^2	F
G^+ bactPLFA	0	i14:0	1	0.391 **	1	1.433×10^8 **
		i15:0	1	0.250 **		
		a15:0	1	0.460 **		
		i16:0	1	0.196 **		
		i17:0	1	0.167 **		
		a17:0	1.001	0.104 **		
G^- bactPLFA	-2.543×10^{-5}	16:1ω5c	1	0.065 **	1	5.641×10^{10} **
		16:1ω7c	1	0.153 **		
		cy17:0	1	0.083 **		
		17:1ω8c	1	0.065 **		
		18:1ω7c	1	0.118 **		
		18:1ω9c	1	0.673 **		
		cy19:0	1	0.212 **		
F/B	0.218	i16:0	−0.046	−0.152 **	0.978	394.789 **
		cy17:0	−0.201	−0.45 **		
		cy19:0	−0.018	−0.102 *		
		18:2ω6,9c	0.048	1.023 **		
G^+/G^-	0.861	a15:0	0.263	0.782 **	0.926	96.345 **
		18:1ω7c	−0.240	−0.293 **		
		18:1ω9c	−0.029	−0.201 **		
		cy19:0	−0.112	−0.246 **		

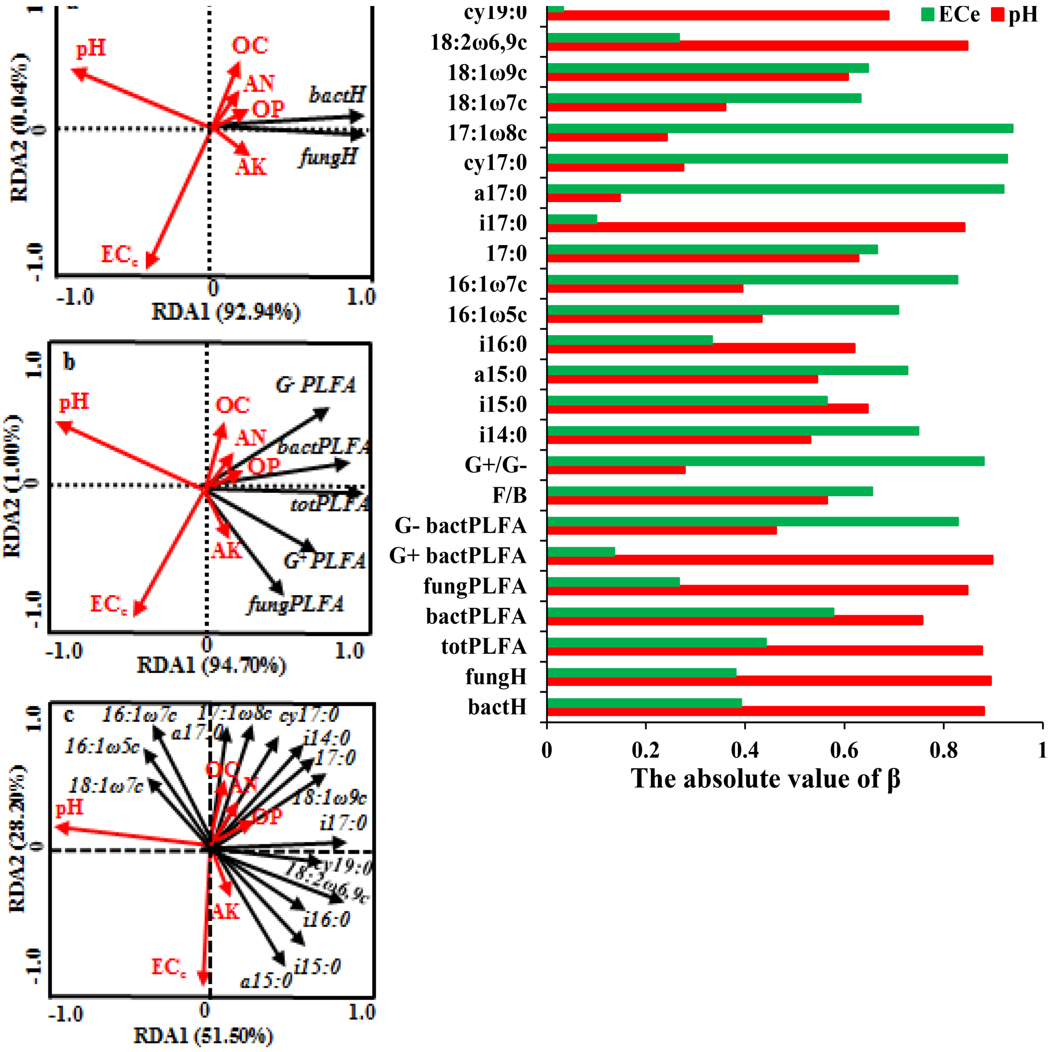


Figure 5. Redundancy analysis (RDA) ordination biplot and determination variable based on the effects of soil properties on microbial parameters. a, the relationships between microbial diversity and soil properties. b, the relationships between microbial PLFA biomass and soil properties. c, the relationships between 15 PLFAs and soil properties. d, the variables with the highest determination coefficient (the absolute value of β) of soil pH and EC_e.

4. Discussion

4.1. Changes in Soil Properties and Microbial Community under Seawater Irrigation

Seawater irrigation typically introduces more soluble salts into the soil, leading to increased salt accumulation [8,20,22,63]. Soil EC_e and pH are critical chemical indicators of soil salinity and alkalinity [8]. As hypothesized, this study demonstrated that seawater irrigation significantly elevated soil pH, EC_e, and salt content, likely due to the high sodium (Na^+) concentration and elevated pH (8.0–8.5) of the irrigation water. This process, often termed secondary salinization, is the core chemical change under seawater irrigation. In contrast, previous studies reported that saline ice irrigation reduced soil salinity and pH [3,30], while seawater irrigation had a relatively minor impact on soil salinity [6,12]. This discrepancy may stem from increased soil moisture and gradual salinity reduction caused by saline ice irrigation and heavy rainfall during the growth period. In this study, seawater irrigation significantly decreased soil OC, AN, and OP, consistent with prior observations [14]. This reduction is likely due to altered microbial decomposition processes, nutrient leaching, or changes in soil chemistry that make these nutrients less accessible under seawater irrigation. However, the increase in AK observed here contrasts with the earlier finding that saline water irrigation reduced AK [14]. This difference may arise from the higher potassium content in seawater compared to saline water.

Consistent with our hypothesis, bactH, fungH, totPLFA, bactPLFA, and G^- bactPLFA significantly decreased with rising irrigation water salinity, while fungPLFA, F/B, and G^+/G^- increased markedly. One explanation is that salt stress from seawater irrigation disrupts microbial community structure, reducing microbial populations by killing sensitive microorganisms. Similar results have been documented: long-term seawater irrigation decreased soil microbial biomass [63] due to high EC_e and pH, deteriorating soil physicochemical properties and limiting microbial activity. However, a contrasting finding reported no effect of seawater irrigation on microbial diversity or biomass in sandy soils [6], likely because seasonal heavy rainfall prevented salinity-induced declines. In this study, seawater irrigation significantly increased the concentrations of i15:0, a15:0, i16:0, and 18:2ω6,9c while decreasing i14:0, 16:1ω5c, 16:1ω7c, 17:0, a17:0, cy17:0, 17:1ω8c, 18:1ω7c, 18:1ω9c, and cy19:0. This contrasts with Liu et al. (2019) [6], who observed minimal impact on microbial community composition, possibly because appropriate rainfall maintained moderate soil pH and salinity without causing secondary salinization. These results suggest that seawater irrigation increases soil pH and salinity, reduces nutrient content, and alters microbial communities. However, the extent of these changes can be moderated by factors like subsequent rainfall, which can leach salts and mitigate the salinity buildup. Since this study did not investigate soil physicochemical properties or microbial responses when irrigation water salinity exceeds $3.5\ g\cdot L^{-1}$, further research is needed to determine the salinity threshold for irrigation water and its effects on soil salinization, microbial communities, and crop health.

4.2. Improvement of Gypsum in Soil Properties and Microbial Communities

Adding gypsum to salt-affected soils is an effective strategy for reducing soil salinity [3,64]. Consistent with our hypothesis, gypsum application in the present study significantly reduced soil EC_e and salt content. This effect may be attributed to improved soil structure through cation bridging between clay particles and soil organic matter [65]. Additionally, the calcium ions (Ca^{2+}) released by gypsum replace sodium ions (Na^+) in the soil. As gypsum ($CaSO_4$) dissolves in water, it reacts with NaCl, Na_2CO_3, and $NaHCO_3$ to form Na_2SO_4, $CaCl_2$, $CaCO_3$, and $Ca(HCO_3)_2$. Consequently, soil Na^+ levels decrease, reducing salinity as salt leaching increases due to natural rainfall and irrigation [31,37,38,64,66]. In saline-sodic soils, gypsum application has been shown to reduce soil pH [3,64], and this trend was confirmed in this study. Soil pH decrease occurs because Ca^{2+} from gypsum reacts with bicarbonate (HCO_3^-), carbonate (CO_3^{2-}), and hydroxide (OH^-) ions in the soil, forming calcite ($CaCO_3$) precipitates and releasing protons (H^+: $Ca^{2+} + CO_2 + H_2O \leftrightarrow CaCO_3 + 2H^+$).This process lowers soil pH [36,38,67,68]. Furthermore, sulfate (SO_4^{2-}) ions also contribute to pH reduction from gypsum [69]. As expected, gypsum application increased soil OC, AN, and OP in this study, aligning with previous findings [70–72]. This increase likely stems from enhanced total plant biomass, which raises OC and total nitrogen levels through plant residue incorporation into the soil. However, AK was reduced in this study, consistent with observations by Yahya et al. (2022) [49] and Son et al. (2017) [73], due to K^+ leaching after its substitution by Ca^{2+} from gypsum.

Gypsum directly ameliorates soil physicochemical properties by reducing salinity, improving structure, and modifying pH, and indirectly creates a more hospitable environment that stimulates microbial growth [23,74] and alters the community structure [41]. In this study, gypsum significantly increased bactH, fungH, totPLFA, bactPLFA, fungPLFA, G^+ bactPLFA, G^- bactPLFA, and F/B and G^+/G^-. These results suggest that certain microorganisms are more sensitive to gypsum under field conditions, corroborating prior literature [41,71]. A possible mechanism for gypsum's stimulation of microbial parameters is its ability to enhance soil aggregates through cation bridging between clay particles and organic matter, creating a favorable environment for microbial survival [65]. This process increases microbial biomass and activity [63]. Additionally, gypsum significantly increased concentrations of i14:0, i15:0, a15:0, i16:0, 17:0, i17:0, cy17:0, 17:1ω8c, 18:1ω9c, cy19:0, and 18:2ω6,9c while reducing 16:1ω5c, 16:1ω7c, and 18:1ω7c in this study. These changes may be driven by gypsum-induced shifts in soil pH and salinity [75–77]. In summary, gypsum's effects on soil microbial diversity, biomass, community structure, and composition are likely to result from both direct impacts and indirect effects via pH and salinity changes. By improving soil physicochemical properties and microbial communities, gypsum holds significant potential for application in seawater irrigation agriculture.

4.3. The Conjunctive Effects of Gypsum Application and Seawater Irrigation

While numerous studies have examined the individual effects of seawater irrigation [2,6,8,23] or gypsum application [43,63] on soil properties and various crops in saline environments, research on their combined impact on soil physicochemical and biological properties remains limited. This study demonstrated that the conjunctive application of gypsum and seawater irrigation jointly and effectively regulated soil pH and salinity in coastal saline soils, presumably through a series of integrated chemical and physical processes. Chemically, gypsum dissolution releases calcium ions (Ca^{2+}) which displace sodium ions (Na^{+}) from soil colloids, mitigating sodicity. Crucially, these Ca^{2+} ions react with bicarbonate, carbonate, and hydroxide ions (from the soil and seawater), precipitating calcite ($CaCO_3$) and releasing protons (H^{+}), directly lowering soil pH. Concurrently, sulfate ions (SO_4^{2-}) from gypsum contribute to pH reduction, and gypsum reacts with sodium salts to form more soluble salts like Na_2SO_4. Physically, seawater irrigation provides the water vehicle for leaching, while the Ca^{2+} from gypsum promotes soil flocculation, improving structure and infiltration. This improved physical condition facilitates the removal of the transformed and displaced salts (e.g., NaCl, Na_2SO_4) from the root zone. Consistent with our hypothesis, gypsum application significantly reduced soil EC_e, pH, and salt content under seawater irrigation. This suggests that the strategic combination of gypsum amendment and seawater irrigation can mitigate the progression of soil salinization. The observed decrease in soil pH aligns with previous findings [14,19]. However, the reduction in soil EC_e and salt content reported here contrasts with some earlier observations [14,19], a discrepancy that may be attributed to differences in soil type, as the efficacy of gypsum is highly dependent on soil characteristics.

Compared to the freshwater irrigation treatment in this study, the combined application of gypsum and seawater irrigation significantly decreased soil OC, AN, and OP contents, while increasing AK content. This supports our hypothesis regarding the nutrient dynamics under combined stress. The underlying mechanisms for these changes are threefold: First, the high salinity associated with seawater irrigation inhibits microbial activity, thereby slowing the decomposition of organic matter [78,79]. Second, salinity stress reduces plant productivity, which diminishes the input of organic nitrogen and phosphorus into the soil, leading to lower OC, AN, and OP levels [80]. Finally, the increase in soil AK is likely due to the direct input of potassium ions (K^{+}) from the irrigation seawater itself.

Diverging from some previous observations [47,71], the combined application of gypsum and seawater irrigation in this study significantly reduced both bactH and fungH compared to freshwater irrigation treatments. This discrepancy may be attributed to differences in irrigation water quality, specifically the use of seawater in this study versus wastewater in the cited works. Furthermore, the combined treatment significantly decreased totPLFA, bactPLFA, and G^{-} bactPLFA, while markedly increasing G^{+} bactPLFA, F/B, and G^{+}/G^{-}. Two primary mechanisms may explain these shifts in microbial biomass and community structure. First, the excessive salinity stress induced by seawater irrigation can cause cell lysis and death in salt-intolerant microorganisms [81]. It is well-established that fungi often exhibit greater salinity tolerance than bacteria in saline soils [75,76], and many G^{+} bacteria possess adaptive strategies, such as spore formation, to survive under high-salinity conditions [82]. Second, gypsum applications may provide a mitigating effect by supplying abundant Ca^{2+} to the soil solution. This promotes effective proton exchange [24] and helps to prevent a rise in soil pH [68], thereby partially offsetting the adverse impacts of salt stress on the soil microbial community during seawater irrigation [77,83]. As our hypothesized, the conjunctive use of gypsum and seawater irrigation significantly altered the soil microbial community composition, specifically affecting the concentrations of i14:0, 17:0, i17:0, 18:1ω7c, cy19:0, i15:0, a15:0, and i16:0 in this study. However, contrary to our expectations, no additive effect of the combined treatment was observed on the PLFAs 16:1ω5c, 16:1ω7c, a17:0, cy17:0, 17:1ω8c, 18:1ω9c, and 18:2ω6,9c.

In a word, the synergistic mechanism between gypsum and seawater irrigation in coastal saline soils functions through the coordinated modification of two critical abiotic factors: soil pH and salinity. Their combined application lowers soil pH and alleviates soil salinity, which together act as direct environmental filters to reshape the microbial community structure. Given the dynamic nature of soil pH and salinity over the long term and across seasons, further multi-scale investigations are urgently needed to elucidate the synergistic effects of gypsum application and seawater irrigation on coastal saline soils in complex climate conditions. Such research is crucial for verifying the combined role of soil pH and salinity in shaping microbial communities.

4.4. Linking the Microbial Parameters to pH and Salinity

The diversity, biomass, community structure, and composition of soil microorganisms are closely related to soil pH and salinity [24,28,41,47,83–85]. Specifically, soil pH was strongly and negatively correlated with a broad spectrum of microbial vitality indicators, including bactH, fungH, totPLFA, bactPLFA, fungPLFA, G^+ bactPLFA, and G^- bactPLFA in this study. This establishes soil pH as the primary environmental determinant for overall microbial abundance and diversity. This study challenges previous perspectives that salinity was the dominant environmental factor shaping microbial communities [51], overshadowing pH and other physicochemical properties, and that pH was the primary determinant of bacterial communities rather than fungal communities [77]. It is noteworthy that a previous study reported a positive relationship between pH and G^- bactPLFA in acid soils [86]. This discrepancy likely stems from differences in soil type, which appears to be a primary determinant of microbial community responses to pH shifts induced by amendments like gypsum. Simultaneously, soil salinity exhibits a more nuanced, pattern-driven influence. While EC_e was negatively correlated with general microbial metrics (diversity, total and bacterial biomass, and notably G^- bactPLFA) in this study, it showed positive correlations with two key community structural ratios: F/B and G^+/G^-. This pattern indicated that soil salinity selectively suppressed salt-sensitive G^- bacteria more than the relatively salt-tolerant G^+ bacteria and fungi. The observed shifts are consistent with an increase in F/B [75,76] and an overall reduction in microbial biomass and diversity [24] in coastal areas with high salinity soils, forming independently of soil pH or through interactions with salinity the microbial communities [81,87,88]. These findings indicate that soil salinity emerges as the dominant factor driving G^- bactPLFA, F/B, and G^+/G^-. Consequently, the observed microbial shifts are directly attributed to the specific modifications in the soil chemical environment (lowered pH and moderated salinity) brought about by the gypsum-seawater synergy, ultimately selecting for a more stress-tolerant microbial community that contributes to improved ecological function.

As highlighted in prior studies on the relationship between PLFAs and soil microbiota [16,89,90], our stepwise linear regression analysis revealed that i17:0 was the primary contributor to bactH, while 18:2ω6,9c had the strongest influence on fungH. These findings suggested that shifts in bacterial diversity were predominantly driven by changes in i17:0, whereas fungal diversity dynamics were primarily governed by 18:2ω6,9c. Additionally, our analysis identified key fatty acids as major drivers of other microbial indicators: 18:1ω9c had the greatest impact on totPLFA, bactPLFA, and G^- bactPLFA. a15:0 was the dominant contributor to G^+/G^-. 18:2ω6,9c (also linked to fungH) had the strongest effect on F/B. These results indicated that: Changes in totPLFA, bactPLFA, and G^- bactPLFA were primarily driven by 18:1ω9c; Shifts in G^+ bactPLFA and G^+/G^- were mainly influenced by a15:0; Variations in fungH and F/B were predominantly caused by 18:2ω6,9c. Thus, soil pH indirectly affects bactH through i17:0 and fungH and F/B via 18:2ω6,9c, while soil salinity primarily impacts G^+ bactPLFA and G^+/G^- through a15:0, and influences totPLFA, bactPLFA, and G^- bactPLFA due to 18:1ω9c.

5. Conclusions

Improving coastal saline soil is essential for boosting agricultural productivity in these regions. The present study investigated the combined effects of gypsum application and seawater irrigation on coastal saline soils, aiming to evaluate their effectiveness in enhancing soil pH, reducing salinity, improving nutrient availability, and reshaping microbial communities. Our findings demonstrate that gypsum application significantly enhanced rice grain yield by improving key yield components, while seawater irrigation alone reduced them. The synergistic use of gypsum and seawater irrigation also successfully improved soil pH, salinity, and nutrient levels, thereby making significant changes in microbial community structure. These results hold substantial significance for understanding the mechanistic relationships between microbial parameters and abiotic factors (e.g., pH, salinity, nutrients). Such insights are critical for developing practical strategies to enhance soil fertility and agricultural productivity in coastal saline environments. In summary, gypsum plays a pivotal role in reshaping microbial communities by modulating soil pH and salinity. This underscores the importance of integrating gypsum application with seawater irrigation as a sustainable approach to improving coastal saline-alkali lands and ultimately increasing crop yields.

Author Contributions

Q.F.: Writing—original draft, review & editing, Methodology, Investigation, Conceptualization, Project administration, Data curation, Funding acquisition. G.Q.: Writing—review & editing, Methodology, Supervision, Investigation. B.G.: Writing—review & editing, Methodology, Investigation. J.Z.: Writing—review & editing, Resources, Investigation. J.L.: Supervision, Resources. X.C.: Supervision, Writing—review & editing, Investigation. All authors have read and agreed to the published version of the manuscript.

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Not applicable.

Informed Consent Statement

Not applicable.

Data Availability Statement

Data will be made available on request.

Conflicts of Interest

The authors declare no conflict of interests.

Use of AI and AI-Assisted Technologies

No AI tools were utilized for this paper.

References

1. Arjmand Sajjadi, S.; Mahmoodabadi, M. Aggregate breakdown and surface seal development influenced by rain intensity, slope gradient and soil particle size. *Solid Earth* **2015**, *6*, 311–321. https://doi.org/10.5194/se-6-311-2015.
2. Chaudhary, D.R.; Rathore, A.P.; Jha, B. Effects of seawater irrigation on soil microbial community structure and physiological function. *Int. J. Environ. Sci. Technol.* **2016**, *13*, 2199–2208. https://doi.org/10.1007/s13762-016-1047-7.
3. Zhang, Y.; Yang, J.; Yao, R.; et al. Short-term effects of biochar and gypsum on soil hydraulic properties and sodicity in a saline-alkali soil. *Pedosphere* **2020**, *30*, 694–702. https://doi.org/10.1016/S1002-0160(18)60051-7.
4. Chi, C.M.; Zhao, C.W.; Sun, X.J.; et al. Reclamation of saline-sodic soil properties and improvement of rice (*Oriza sativa* L.) growth and yield using desulfurized gypsum in the west of Songnen Plain, northeast China. *Geoderma* **2012**, *187*, 24–30. https://doi.org/10.1016/j.geoderma.2012.04.005.
5. Li, Y.; Hu, Y.; Yan, C.; et al. pH and salinity are the dominant limiting factors for the application of mariculture sludge to paddy soil. *Appl. Soil Ecol.* **2022**, *175*, 104463. https://doi.org/10.1016/j.apsoil.2022.104463.
6. Liu, C.; Huang, L.P.; Liu, M.L.; et al. Effects of seawater irrigation on fruit quality of grapevine, soil properties and microbial diversity. *Sci. Hortic.* **2019**, *253*, 80–86. https://doi.org/10.1016/j.scienta.2019. 04.022.
7. Zhang, W.; Wang, C.; Xue, R.; et al. Effects of salinity on the soil microbial community and soil fertility. *J. Integr. Agric.* **2019**, *18*, 1360–1368. https://doi.org/10.1016/S2095-3119(18)62077-5.
8. Zhang, J.; Wang, H.; Feng, D.; et al. Evaluating the impacts of long-term saline water irrigation on soil salinity and cotton yield under plastic film mulching: A 15-year field study. *Agric. Water Manag.* **2024**, *293*, 108703. https://doi.org/10.1016/j.agwat.2024.108703.
9. Di Baccio, D.; Navari-Izzo, F.; Izzo, R. Seawater irrigation: Antioxidant defence responses in leaves and roots of a sunflower (*Helianthus annuus* L.) ecotype. *J. Plant Physiol.* **2004**, *161*, 1359–1366. https://doi.org/10.1016/j.jplph.2003.07.001.
10. Ghadiri, H.; Dordipour, I.; Bybordi, M.; et al. Potential use of Caspian Sea water for supplementary irrigation in northern Iran. *Agric. Water Manag.* **2006**, *79*, 209–224. https://doi.org/10.1016/j.agwat.2005.04.010.
11. Francois, L.E. Salinity effect on four sunflower hybrids. *Agron. J.* **1996**, *88*, 215–219. https://doi.org/10.2134/agronj1996.00021962008800020016x.
12. Wan, S.; Kang, Y.; Wang, D.; et al. Effect of saline water on cucumber (*Cucumis sativus* L.) yield and water use under drip irrigation in North China. *Agric. Water Manag.* **2010**, *98*, 105–113. https://doi.org/10.1016/j.agwat.2010.08.003.
13. Yarami, N.; Sepaskhah, A.R. Saffron response to irrigation water salinity, cow manure and planting method. *Agric. Water*

Manag. **2015**, *150*, 57–66. https://doi.org/10.1016/j.agwat.2014.12.004.

14. Cao, Y.; Gao, Y.; Li, J.; et al. Straw composts, gypsum and their mixtures enhance tomato yields under continuous saline water irrigation. *Agric. Water Manag.* **2019**, *223*, 105721. https://doi.org/10.1016/j.agwat.2019.105721.
15. Chen, L.; Li, C.; Feng, Q.; et al. Shifts in soil microbial metabolic activities and community structures along a salinity gradient of irrigation water in a typical arid region of China. *Sci. Total Environ.* **2017**, *598*, 64–70. https://doi.org/10.1016/j.scitotenv.2017.04.105.
16. Chowdhury, N.; Marschner, P.; Burns, R.G. Soil microbial activity and community composition: Impact of changes in matric and osmotic potential. *Soil Biol. Biochem.* **2011**, *43*, 1229–1236. https://doi.org/10.1016/j.soilbio.2011.02.012.
17. Kamble, P.N.; Gaikwad, V.B.; Kuchekar, S.R.; et al. Microbial growth, biomass, community structure and nutrient limitation in high pH and salinity soils from Pravaranagar (India). *Eur. J. Soil Biol.* **2014**, *65*, 87–95. https://doi.org/10.1016/j.ejsobi.2014.10.005.
18. Sall, S.N.; Ndour, N.Y.B.; Diedhiou-Sall, S.; et al. Microbial response to salinity stress in a tropical sandy soil amended with native shrub residues or inorganic fertilizer. *J. Environ. Manag.* **2015**, *161*, 30–37. https://doi.org/10.1016/j.jenvman.2015.06.017.
19. Wang, Q.; Men, L.; Gao, L.; et al. Effect of grafting and gypsum application on cucumber (*Cucumis sativus* L.) growth under saline water irrigation. *Agric. Water Manag.* **2017**, *188*, 79–90. https://doi.org/10.1016/j.agwat.2017.04.003.
20. Wang, X.; Yang, J.; Liu, G.; et al. Impact of irrigation volume and water salinity on winter wheat productivity and soil salinity distribution. *Agric. Water Manag.* **2015**, *149*, 44–54. https://doi.org/10.1016/j.agwat.2014.10.027.
21. Wichern, J.; Wichern, F.; Joergensen, R.G. Impact of salinity on soil microbial communities and the decomposition of maize in acidic soils. *Geoderma* **2006**, *137*, 100–108. https://doi.org/10.1016/j.geoderma.2006.08.001.
22. Machekposhti, M.F.; Shahnazari, A.; Ahmadi, M.Z.; et al. Effect of irrigation with sea water on soil salinity and yield of oleic sunflower. *Agric. Water Manag.* **2017**, *188*, 69–78. https://doi.org/10.1016/j.agwat.2017.04.002.
23. Vera, A.; Moreno, J.L.; Garcia, C.; et al. Agro-physiological and soil microbial responses to desalinated seawater irrigation in two crops. *Ecotoxicol. Environ. Saf.* **2023**, *250*, 114507. https://doi.org/10.1016/j.ecoenv.2023.
24. Chen, H.; Ma, K.; Huang, Y.; et al. Significant response of microbial community to increased salinity across wetland ecosystems. *Geoderma* **2022**, *415*, 115778. https://doi.org/10.1016/j.geoderma.2022.115778.
25. Haj-Amor, Z.; Araya, T.; Kim, D.G.; et al. Soil salinity and its associated effects on soil microorganisms, greenhouse gas emissions, crop yield, biodiversity and desertification: A review. *Sci. Total Environ.* **2022**, *843*, 156946. https://doi.org/10.1016/j.scitotenv.2022.156946.
26. Heng, T.; Yang, L.; Hermansen, C.; et al. Linking microbial community compositions to cotton nitrogen utilization along soil salinity gradients. *Field Crop Res.* **2022**, *288*, 108697. https://doi.org/10.1016/j.fcr.2022.108697.
27. Zhao, F.; Xu, K.D. Microbial genetic diversity and ciliate community structure along an environmental gradient in coastal soil. *Eur. J. Protistol.* **2013**, *49*, 516–525. https://doi.org/10.1016/j.ejop.2013.01.002.
28. Yan, D.; Long, X.; Ye, L.; et al. Effects of salinity on microbial utilization of straw carbon and microbial residues retention in newly reclaimed coastal soil. *Eur. J. Soil Biol.* **2021**, *107*, 103364. https://doi.org/10.1016/j.ejsobi.2021.103364.
29. El-Kadya, A.F.Y.; Borham, T.I. Sustainable cultivation under saline irrigation water: Alleviating salinity stress using different management treatments on *Terminalia arjuna* (Roxb.) Wight & Arn. *Agric. Water Manag.* **2020**, *229*, 105902. https://doi.org/10.1016/j.agwat.2019.105902.
30. Guo, K.; Liu, X.J. Dynamics of meltwater quality and quantity during saline ice melting and its effects on the infiltration and desalinization of coastal saline soils. *Agric. Water Manag.* **2014**, *139*, 1–6. https://doi.org/10.1016/j.agwat.2014.03.007.
31. Kim, Y.J.; Choo, B.K.; Cho, J.Y. Effect of gypsum and rice straw compost application on improvements of soil quality during desalination of reclaimed coastal tideland soils: Ten years of long-term experiments. *Catena* **2017**, *156*, 131–138. https://doi.org/10.1016/j.catena.2017.04.008.
32. Choudhary, O.P.; Ghuman, B.S.; Singh, B.; et al. Effects of long-term use of sodic water irrigation, amendments and crop residues on soil properties and crop yields in rice–wheat cropping system in a calcareous soil. *Field Crop Res.* **2011**, *121*, 363–372. https://doi.org/10.1016/j.fcr.2011.01.004.
33. Mao, G.; Xu, X.; Chen, Q.; et al. Flue gas desulfurization gypsum byproducts alters cytosolic Ca^{2+} distribution and Ca^{2+}-ATPase activity in leaf cells of oil sunflower in alkaline soil. *J. Plant Interact.* **2014**, *9*, 152–158. https://doi.org/10.1201/9781351027021-14.
34. McKenna, B.A.; Kopittke, P.M.; Macfarlane, D.C.; et al. Changes in soil chemistry after the application of gypsum and sulfur and irrigation with coal seam water. *Geoderma* **2019**, *337*, 782–791. https://doi.org/10.1016/j.geoderma.2018.10.019.
35. Fang, Y.; Pal Singh, B.; Van Zwieten, L.; et al. Additive effects of organic and inorganic amendments can significantly improve structural stability of a sodic dispersive subsoil. *Geoderma* **2021**, *404*, 115281.

https://doi.org/10.1016/j.geoderma.2021.115281.

36. Sundha, P.; Basak, N.; Rai, A.K.; et al. Can conjunctive use of gypsum, city waste composts and marginal quality water rehabilitate saline-sodic soils? *Soil Tillage Res.* **2020**, *200*, 104608. https://doi.org/10.1016/j.still.2020.104608.
37. Xu, X.; Guo, L.; Wang, S.; et al. Effective strategies for reclamation of saline-alkali soil and response mechanisms of the soil-plant system. *Sci. Total Environ.* **2023**, *905*, 167179. https://doi.org/10.1016/j.scitotenv.2023.167179.
38. Wang, Y.; Wang, Z.; Liang, F.; et al. Application of flue gas desulfurization gypsum improves multiple functions of saline-sodic soils across China. *Chemosphere* **2021**, *277*, 130345. https://doi.org/10.1016/j.chemosphere.2021.
39. Chen, J.; Hu, G.; Wang, H.; et al. Leaching and migration characteristics of nitrogen during coastal saline soil remediation by combining humic acid with gypsum and bentonite. *Ann. Agric. Sci.* **2023**, *68*, 1–11. https://doi.org/10.1016/j.aoas.2023.02.001.
40. Mitchell, J.P.; Shennan, C.; Singer, M.J.; et al. Impacts of gypsum and winter cover crops on soil physical properties and crop productivity when irrigated with saline water. *Agric. Water Manag.* **2000**, *45*, 55–71. https://doi.org/10.1016/S0378-3774(99)00070-0.
41. Li, M.; Jiang, L.L.; Sun, Z.J.; et al. Effects of flue gas desulfurization gypsum by-products on microbial biomass and community structure in alkaline–saline soils. *J. Soil Sediment.* **2012**, *12*, 1040–1053. https://doi.org/10.1007/s11368-012-0531-z.
42. Kaur, J.; Choudhary, O.P.; Singh, B. Microbial biomass carbon and some soil properties as influenced by long-term sodic-water irrigation, gypsum, and organic amendments. *Aust. J. Soil Res.* **2008**, *46*, 141–151. https://doi.org/10.1071/SR07108.
43. Wong, V.N.L.; Dalal, R.C.; Greene, R.S.B. Carbon dynamics of sodic and saline soils following gypsum and organic material additions: A laboratory incubation. *Appl. Soil Ecol.* **2009**, *41*, 29–40. https://doi.org/10.1016/j.apsoil.2008.08.006.
44. Cheng, Q., Chang, H., Yang, X.; et al. Salinity and nutrient modulate soil bacterial communities in the coastal wetland of the Yellow River Delta, China. *Environ. Sci. Pollut. Res.* **2021**, *28*, 14621–14631. https://doi.org/10.1007/s11356-020-11626-x.
45. Gao, Y.; Liu, L.; Zhu, P.; et al. Patterns and dynamics of the soil microbial community with gradual vegetation succession in the Yellow River Delta, China. *Wetlands* **2021**, *41*, 9. https://doi.org/10.1007/s11356-020-11626 -x.
46. Liu, L.; Wu, Y.; Yin, M.; et al. Soil salinity, not plant genotype or geographical distance, shapes soil microbial community of a reed wetland at a fine scale in the Yellow River Delta. *Sci. Total Environ.* **2023**, *856*, 159136. https://doi.org/10.1016/j.scitotenv.2022.159136.
47. Dang, Q.; Tan, W.; Zhao, X.; et al. Linking the response of soil microbial community structure in soils to long-term wastewater irrigation and soil depth. *Sci. Total Environ.* **2019**, *688*, 26–36. https://doi.org/10.1016/j.scitotenv.2019.06.138.
48. Dini-Andreote, F.; Pylro, V.S.; Baldrian, P.; et al. Ecological succession reveals potential signatures of marine–terrestrial transition in salt marsh fungal communities. *ISME J.* **2016**, *10*, 1984–1997. https://doi.org/10.1038/ismej.2015.254.
49. Yahya, K.E.; Jia, Z.; Luo, W.; et al. Enhancing salt leaching efficiency of saline-sodic coastal soil by rice straw and gypsum amendments in Jiangsu coastal area. *Ain Shams Eng. J.* **2022**, *13*, 101721. https://doi.org/10.1016/j.asej.2022.101721.
50. Yao, Z.; Du, S.; Liang, C.; et al. Bacterial community assembly in a typical estuarine marsh with multiple environmental gradients. *Appl. Environ. Microbiol.* **2019**, *85*, e02602-18. https://doi.org/10.1128/AEM.02602-18.
51. Lozupone, C.A.; Knight, R. Global patterns in bacterial diversity. *Proc. Natl. Acad. Sci. USA* **2007**, *104*, 11436–11440. https://doi.org/10.1073/pnas.0611525104.
52. Fu, Q.L.; Liu, C.; Ding, N.F.; et al. Soil microbial communities and enzyme activities in a reclaimed coastal soil chronosequence under rice-barley cropping. *J. Soil Sediment.* **2012**, *12*, 1134–1144. https://doi.org/10.1007/s11368-012-0544-7.
53. Li, J.; Pu, L.; Han, M.; et al. Soil salinization research in China: Advances and prospects. *J. Geogr. Sci.* **2014**, *24*, 943–960. https://doi.org/10.1007/s11442-014-1130-2.
54. Fu, Q.L.; Ding, N.F.; Liu, C.; et al. Soil development under different cropping systems in a reclaimed coastal soil chronosequence. *Geoderma* **2014**, *230–231*, 50–57. https://doi.org/10.1016/j.geoderma.2014.03.026.
55. Marschner, P.; Fu, Q.L.; Rengel, Z. Manganese availability and microbial populations in the rhizosphere of wheat genotypes differing in tolerance to Mn deficiency. *J. Plant Nutr. Soil Sci.* **2003**, *166*, 712–718. https://doi.org/10.1002/jpln. 200320333.
56. Williams, M.A. Response of microbial communities to water stress in irrigated and drought-prone tall grass prairie soils. *Soil Biol. Biochem.* **2007**, *39*, 2750–2757. https://doi.org/10.1016/j.soilbio.2007.05.025.

57. Budge, K.; Leifeld, J.; Egli, M.; et al. Soil microbial communities in (sub) alpine grasslands indicate a moderate shift towards new environmental conditions 11 years after soil translocation. *Soil Biol. Biochem.* **2011**, *43*, 1148–1154. https://doi.org/10.1016/j.soilbio.2011.02.001.
58. Li, J.; Li, Z.A.; Wang, F.M.; et al. Effects of nitrogen and phosphorus addition on soil microbial community in a secondary tropical forest of China. *Biol. Fert. Soils.* **2015**, *51*, 207–215. https://doi.org/10.1007/s00374-014-0964-1.
59. Ge, T.D.; Chen, X.J.; Yuan, H.Z.; et al. Microbial biomass, activity, and community structure in horticultural soils under conventional and organic management strategies. *Eur. J. Soil Biol.* **2013**, *58*, 122–128. https://doi.org/10.1016/j.ejsobi.2013.07.005.
60. Xiao, L.; Liu, G.B.; Xue, S.; et al. Soil microbial community composition during natural recovery in the Loess Plateau, China. *J. Integr. Agric.* **2013**, *12*, 1872–1883. https://doi.org/10.1016/S2095-3119(13)60399-8.
61. Bååth, E.; Anderson, T.H. Comparison of soil fungal/bacterial ratios in a pH gradient using physiological and PLFA based techniques. *Soil Biol. Biochem.* **2003**, *35*, 55–963. https://doi.org/10.1016/S0038-0717(03)00154-8.
62. Uyanik, G.K.; Güler, N. A study on multiple linear regression analysis. *Procedia Soc. Behav. Sci.* **2013**, *106*, 234–240. https://doi.org/10.1016/j.sbspro.2013.12. 027.
63. Choudhary, O.P.; Gill, J.K.; Singh, B. Water-extractable carbon pools and microbial biomass carbon in sodic water-irrigated soils amended with gypsum and organic manures. *Pedosphere* **2013**, *23*, 88–97. https://doi.org/10.1016/S1002-0160(12)60083-6.
64. Mao, Y.; Li, X.; Dick, W.A.; et al. Remediation of saline-sodic soil with flue gas desulfurization gypsum in a reclaimed tidal flat of southeast China. *J. Environ. Sci.* **2016**, *45*, 224–232. https://doi.org/10.1016/j.jes.2016.01.006.
65. Qadir, M.; Qureshi, R.H.; Ahmad, N. Reclamation of a saline-sodic soil by gypsum and Leptochloa fusca. *Geoderma* **1996**, *74*, 207–217. https://doi.org/10.1016 /S0016-7061(96)00061-4.
66. Chen, L.; Ramsier, C.; Bigham, J.; et al. Oxidation of FGD-$CaSO_3$ and effect on soil chemical properties when applied to the soil surface. *Fuel* **2009**, *88*, 1167–1172. https://doi.org/10.1016/j.fuel.2008.07.015.
67. Basak, N.; Sheoran, P.; Sharma, R.; et al. Gypsum and pressmud amelioration improve soil organic carbon storage and stability in sodic agroecosystems. *Land Degrad. Dev.* **2021**, *32*, 4430–4444. https://doi.org/10.1002/ldr.4047.
68. Tao, J.; Wu, L.H.; Liu, X.J.; et al. Effect of brackish ice on salt and nutrient contents of saline soil in flue-gas desulfurization gypsum amended, raised bed agroecosystem. *Soil Sci. Soc. Am. J.* **2014**, *78*, 1734–1740. https://doi.org/10.2136/sssaj2014.03.0095.
69. Shaaban, M.; Wu, Y.; Núnez-Delgado, A.; et al. Enzyme activities and organic matter mineralization in response to application of gypsum, manure and rice straw in saline and sodic soils. *Environ. Res.* **2023**, *224*, 115393. https://doi.org/10.1016/j.envres.2023.115393.
70. Luo, S.; Wang, S.; Tian, L.; et al. Aggregate-related changes in soil microbial communities under different ameliorant applications in saline-sodic soils. *Geoderma* **2018**, *329*, 108–117. https://doi.org/10.1016/j.geoderma.2018.05.023.
71. Somenahally, A.C.; McLawrence, J.; Chaganti, V.N.; et al. Response of soil microbial Communities, inorganic and organic soil carbon pools in arid saline soils to alternative land use practices. *Ecol. Indic.* **2023**, *150*, 110227. https://doi.org/10.1016/j.ecolind.2023.110227.
72. Walia, M.K.; Dick, W.A. Selected soil physical properties and aggregate -associated carbon and nitrogen as influenced by gypsum, crop residue, and glucose. *Geoderma* **2018**, *320*, 67–73. https://doi.org/10.1016/j.geoderma.2018.01.022.
73. Son, J.K.; Shin, W.T.; Lee, S.H.; et al. Reclamation of a coastal reclaimed tidal land soil by gypsum and rice straw. *Arch. Agron. Soil Sci.* **2017**, *63*, 761–770. https://doi.org/10.1080/03650340.2016.1241393.
74. Wu, Y.; Li, Y.; Zheng, C.; et al. Organic amendment application influence soil organism abundance in saline alkali soil. *Eur. J. Soil Biol.* **2013**, *54*, 32–40. https://doi.org/10.1016/j.ejsobi.2012.10.006.
75. Rath, K.M.; Fierer, N.; Murphy, D.V.; et al. Linking bacterial community composition to soil salinity along environmental gradients. *ISME J.* **2019**, *13*, 836–846. https://doi.org/10.1038/s41396-018-0313-8.
76. Rath, K.M.; Murphy, D.N.; Rousk, J. The microbial community size, structure, and process rates along natural gradients of soil salinity. *Soil Biol. Biochem.* **2019**, *138*, 107607. https://doi.org/10.1016/j.soilbio.2019.107607.
77. Rousk, J.; Bååth, E.; Brookes, P.C.; et al. Soil bacterial and fungal communities across a pH gradient in an arable soil. *ISME J.* **2010**, *4*, 1340–1351. https://doi.org/10.1038 /ismej.2010.58.
78. Shahariar, S.; Farrell, R.; Soolanayakanahally, R.; et al. Elevated salinity and water table drawdown significantly affect greenhouse gas emissions in soils from contrasting land-use practices in the prairie pothole region. *Biogeochemistry* **2021**, *155*, 127–146. https://doi.org/10.1007/s10533-021-00818-3.
79. She, R.; Yu, Y.; Ge, C.; et al. Soil texture alters the impact of salinity on carbon mineralization. *Agronomy* **2021**, *11*, 128. https://doi.org/10.3390/agronomy11010128.
80. Bhardwaj, A.K.; Mishra, V.K.; Singh, A.K.; et al. Soil salinity and land use-land cover interactions with soil carbon in a salt-affected irrigation canal command of Indo-Gangetic Plain. *Catena* **2019**, *180*, 392–400. https://doi.org/10.1016/j.catena.2019.05.015.

81. Li, J.; Chen, Q.; Li, Q.; et al. Influence of plants and environmental variables on the diversity of soil microbial communities in the Yellow River Delta Wetland, China. *Chemosphere* **2021**, *274*, 129967. https://doi.org/10.1016/j.chemosphere.2021.
82. Marquez, M.C.; Sanchez-Porro, C.; Ventosa, A. Halophilic and haloalkaliphilic, aerobic endospore-forming bacteria in soil. In *Endospore-Forming Soil Bacteria*; Logan, N.A., DeVos, P., Eds.; Springer: Berlin, Germany, 2011; pp. 309–339.
83. Lauber, C.L.; Hamady, M.; Knight, R.; et al. Pyrosequencing-based assessment of soil pH as a predictor of soil bacterial community structure at the continental scale. *Appl. Environ. Microbiol.* **2009**, *75*, 5111–5120. https://doi.org/10.1128/AEM.00335-09.
84. Elgharably, A.; Marschner, P. Microbial activity and biomass and N and P availability in a saline sandy loam amended with inorganic N and lupin residues. *Eur. J. Soil Biol.* **2011**, *47*, 310–315. https://doi.org/10.1016/j.ejsobi.2011.07.005.
85. Hua, J.; Feng, Y.; Jiang, Q.; et al. Shift of bacterial community structure along different coastal reclamation histories in Jiangsu. Eastern China. *Sci. Rep.* **2017**, *7*, 10096. https://doi.org/10.1038/s41598-017-10608-3.
86. Frostegård, Å.; Bååth, E.; Tunlid, A. Shifts in the structure of soil microbial communities in limed forests as revealed by phospholipid fatty acid analysis. *Soil Biol. Biochem.* **1993**, *25*, 723–730. https://doi.org/10.1016/0038-0717(93)90113-P.
87. Wang, J.; Wang, J.; Zhang, Z.; et al. Shifts in the bacterial population and ecosystem functions in response to vegetation in the Yellow River Delta wetlands. *Msystems* **2020**, *5*, e00412-20. https://doi.org/10.1128/mSystems.00412-20.
88. Zhao, S.; Liu, J.J.; Banerjee, S.; et al. Not by salinity alone: How environmental factors shape fungal communities in saline soils. *Soil Sci. Soc. Am. J.* **2019**, *83*, 1387–1398. https://doi.org/10.2136/sssaj2019.03.0082.
89. Elmajdoub, B.; Marschner, P. Responses of soil microbial activity and biomass to salinity after repeated additions of plant residues. *Pedosphere* **2015**, *25*, 177–185. https://doi.org/10.1016/S1002-0160(15)60002-9.
90. Pankhurst, C.E.; Yu, S.; Hawke, B.G.; et al. Capacity of fatty acid profiles and substrate utilization patterns to describe differences in soil microbial communities associated with increased salinity or alkalinity at three locations in South Australia. *Biol. Fert. Soils.* **2001**, *33*, 204–217. https://doi.org/10.1007/s003740000309.