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Spartina alterniflora-Derived Biochar Alters Biomass Allocation and Root Traits of Native *Scirpus mariqueter*

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Abstract: Coastal wetlands provide vital ecosystem services, yet large-scale removal of invasive *Spartina alterniflora* disrupts soil carbon pools and fragments habitats. Converting this biomass to biochar may enhance restoration outcomes, though ecological effects remain poorly understood. We evaluated how *Spartina alterniflora*-derived biochar (0%, 0.5%, 1%, and 3%) influences growth performance, clonal reproduction, root morphology, and rhizosphere properties of native *Scirpus mariqueter*. Moderate biochar addition (1%) significantly boosted plant performance, increasing total biomass by 64.5%, aboveground biomass by 36.7%, and belowground biomass by 115.0%, while root length increased by 135.8%. Biochar improved soil moisture and nutrient availability, including nitrate nitrogen (NO_3^--N), ammonium nitrogen (NH_4^+-N), and available phosphorus (AP), while stimulating nitrification and promoting clonal propagation. In contrast, high-dose biochar (3%) elevated soil salinity and electrical conductivity, leading to suppressed plant growth and reproductive allocation. Correlation analysis revealed strong positive associations between root volume and soil nutrient levels. Our findings demonstrate that moderate application of *Spartina alterniflora*-derived biochar enhances plant productivity and soil function, potentially improving carbon sequestration in restored coastal wetlands. This study provides insights into ecological recycling of invasive biomass and supports biochar as a viable tool for sustainable wetland restoration, though potential risks at high concentrations warrant further investigation.

Keywords: allochthonous inputs; carbon sequestration; coastal wetlands; invasive species; native halophyte; root morphology

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Academic Editors: Lele Liu, Yaolin Guo, Youzheng Zhang and Weihua Guo

Received: 17 April 2025
Revised: 15 May 2025
Accepted: 16 May 2025
Published: 18 May 2025

Citation: Tang, Y.; Gao, J.; Jiang, P.; Li, J.; Wu, M.; Jiao, S.; Zhang, L.; Li, N.; Shao, X. *Spartina alterniflora*-Derived Biochar Alters Biomass Allocation and Root Traits of Native *Scirpus mariqueter*. *Diversity* **2025**, *17*, 357. https://doi.org/10.3390/d17050357

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1. Introduction

Coastal wetlands are among the most productive and ecologically valuable ecosystems on Earth, offering critical ecosystem services such as biodiversity conservation, climate regulation, and water purification. Owing to their high primary productivity and efficient carbon sequestration capabilities, coastal wetlands are widely recognized as significant natural carbon sinks [1,2]. However, these ecosystems are highly vulnerable to external disturbances. The aggressive invasion of *Spartina alterniflora* has led to a range of ecological consequences, including obstruction of tidal channels, displacement of native species, loss of biodiversity, and degradation of habitats for waterbirds [3,4]. Remote sensing data indicate that approximately 48.3% of China's coastal salt marshes have been invaded

by this species [5]. *Spartina alterniflora* has become the dominant invasive species in the Hangzhou Bay New District, currently occupying approximately 4670 hectares—nearly one-third of the total invaded area in Zhejiang Province. Following its initial appearance in the mid-1990s, the species expanded rapidly, reaching over 5000 hectares by the early 2000s. Although its distribution temporarily declined due to land reclamation, recent monitoring indicates a marked resurgence [6]. These patterns highlight both the aggressive expansion capacity of *Spartina alterniflora* and the urgent need for sustainable, long-term management strategies in heavily invaded coastal regions.

In response, the Chinese government has launched large-scale eradication programs to control the spread of *Spartina alterniflora*. Integrated management strategies have demonstrated greater efficacy than single-method approaches in controlling *Spartina alterniflora*. Techniques combining mowing with subsequent flooding, soil tilling, or shading have proven particularly effective in limiting its spread across both salt marsh and mangrove ecosystems [7]. However, these interventions have also led to unintended ecological consequences, including habitat fragmentation, altered landscape structures, and significant reductions in above- and belowground carbon stocks [8]. These outcomes compromise the carbon sequestration capacity of coastal wetlands and pose challenges to national carbon neutrality targets. Among the various management strategies for *Spartina alterniflora*, converting its biomass into biochar offers a sustainable, dual-purpose approach—supporting both invasive species control and ecological restoration. Recent studies have highlighted its potential to improve soil properties, enhance plant growth, and increase carbon sequestration in coastal salt marshes [9,10]. Evaluating the restoration potential of *Spartina alterniflora*-derived biochar requires examining its effects on native keystone species that are ecologically sensitive to soil and hydrological changes.

Scirpus mariqueter is a perennial halophytic sedge endemic to the coastal wetlands of China, where it functions as a keystone and pioneer species during the early stages of intertidal zone colonization, particularly in the Yangtze River Estuary and Hangzhou Bay. Through its extensive aboveground biomass and belowground rhizome networks, *Scirpus mariqueter* delivers a range of vital ecosystem services, including shoreline stabilization, sediment accretion, wave attenuation, and carbon sequestration. Additionally, it provides essential foraging and nesting habitats for migratory waterbirds, thereby contributing to regional biodiversity and wetland resilience [11,12]. Despite its ecological importance, the distribution of *Scirpus mariqueter* has declined significantly due to escalating anthropogenic pressures, biological invasion by *Spartina alterniflora*, and rising sea levels [13,14]. Recent studies have highlighted the importance of understanding species-specific responses to environmental gradients in order to inform effective restoration strategies [15]. For *Scirpus mariqueter*, factors such as soil salinity, tidal inundation frequency, nutrient availability, and interspecific competition can significantly influence its growth performance, clonal expansion, and reproductive success [16,17]. In the context of climate change and coastal degradation, elucidating the physiological thresholds and adaptive capacity of *Scirpus mariqueter* is essential to support scalable nature-based solutions that enhance ecosystem functionality and contribute to long-term sustainability and blue carbon goals [18,19].

Invasive weeds, once viewed solely as ecological threats, are now recognized as promising feedstocks for biochar production. Biochar derived from such species has been shown to improve soil physicochemical properties, enhance nutrient retention, and promote plant growth, offering a sustainable pathway for biomass valorization and ecosystem restoration [20–24]. In particular, *Spartina alterniflora*-derived biochar transforms invasive biomass into a valuable resource for coastal rehabilitation [25–27]. However, most existing studies have focused on soil nutrient enhancement or individual plant traits, with limited insight into how varying application rates influence plant–soil interactions. The underlying

mechanisms by which biochar affects rhizosphere nutrient dynamics and plant-mediated carbon sequestration remain poorly understood [28,29].

In this study, we conducted a controlled pot experiment to quantify the effects of four biochar application rates (0%, 0.5%, 1%, and 3%) on the performance of *Scirpus mariqueter*. These application levels were determined based on insights from previous studies and the projected requirements for enhancing soil carbon sequestration [22,30]. Specifically, we assessed plant biomass production, reproductive allocation, root morphological traits, and associated changes in soil physicochemical properties. The objectives of this study were twofold: (1) to identify the optimal biochar concentration for enhancing the growth and clonal propagation of *Scirpus mariqueter*, and (2) to elucidate the underlying mechanisms by biochar may enhance plant-driven carbon sequestration. Findings from this research offer a scientific foundation for effective coastal wetland restoration and provide novel insights into the ecological reutilization of invasive plant biomass for sustainable blue carbon management.

2. Materials and Methods

2.1. Study Site and Sediment Collection

Surface sediments were collected from a representative coastal wetland in Hangzhou Bay, eastern China (30°25′–30°50′ N, 121°00′–121°30′ E). The region experiences a subtropical monsoon climate, with a mean annual temperature of 16.2 °C and average annual precipitation of approximately 1100 mm. The tidal regime is semidiurnal. In March 2024, surface sediments (0–20 cm depth) were sampled for use in the pot experiment.

2.2. Biochar Preparation

In 2022, *Spartina alterniflora* was collected from the same wetland. After thorough rinsing, the biomass was air-dried and cut into segments shorter than 5 cm. It was then oven-dried at 60 °C to constant weight, ground using a pulverizer, and sieved through a 60-mesh screen to ensure uniform particle size. The processed material was pyrolyzed at 500 °C for 2 h under oxygen-limited conditions in a muffle furnace to produce biochar. Prior to use, the physicochemical properties of the biochar were characterized. pH and electrical conductivity (EC) were determined in a 1:5 (w/v) biochar-to-deionized water suspension after shaking for 1 h, using a pH meter (FiveEasy Plus FP20, Mettler-Toledo International Inc., Greifensee, Switzerland) and a conductivity meter (DDSJ-319L, Shanghai INESA Scientific Instruments Co., Ltd., Shanghai, China), respectively. Total carbon (TC) and total nitrogen (TN) were analyzed using an elemental analyzer (Vario EL III, Elementar Analysensysteme GmbH, Langenselbold, Germany), and total phosphorus (TP) was measured via colorimetric analysis following acid digestion. The resulting biochar demonstrated a pH of approximately 9.5 and an electrical conductivity (EC) of 2.07 mS/cm. The concentrations of total carbon (TC), total nitrogen (TN), and total phosphorus (TP) were determined to be 490 g/kg, 12.75 g/kg, and 1.68 g/kg, respectively.

2.3. Experimental Design

The experiment was initiated in March 2024 to evaluate the effects of different biochar application rates (0%, 0.5%, 1%, and 3%, w/w) on the growth of *Scirpus mariqueter* and associated soil properties. Biochar amendment treatments were designated as MBCX% (where X = 0.5, 1, or 3% w/w), representing a gradient of application rates. The unamended soil served as the control and was labeled as CK. A 2% application rate was not included in the design in order to establish a clear low–medium–high gradient and to avoid redundant intermediate levels, which have shown marginal differentiation in effect across soil and plant parameters in previous studies [30,31]. Similar dosing schemes (e.g., 0%, 1%, and

3%) have been widely adopted in recent biochar trials to ensure practical feasibility and statistical efficiency. Each treatment, including the control, was replicated five times (n = 5), resulting in a total of 20 independent experimental pots. Each pot (55 cm × 40 cm × 35 cm) was filled with 15 kg of homogenized sediment thoroughly mixed with the designated biochar concentration. Fifteen healthy and morphologically uniform *Scirpus mariqueter* seedlings (5–8 cm in height) were transplanted into each pot. For each pot, data were collected from 15 seedlings, and the mean value was used as one statistical replicate. Accordingly, the number of statistical replicates was consistent with the number of biological replicates (n = 5). Specifically, we assessed plant biomass production, reproductive allocation, root morphological traits, and associated changes in soil physicochemical properties. The pots were maintained in a greenhouse at the Wetland Ecosystem Research Station of Hangzhou Bay under natural light and ambient temperature. Soil moisture was kept at saturation through regular watering. Aside from the biochar treatments, all other management practices were standardized. To minimize edge effects, pots were randomly arranged and rotated 90° clockwise each week. No additional fertilizers or pesticides were applied throughout the experiment to avoid external influences on soil and plant responses.

2.4. Plant and Soil Measurements

After 240 days of growth (harvested on 30 November 2024), plants were harvested and separated into aboveground and belowground parts. Each component was oven-dried at 65 °C to constant weight to determine total, shoot, and root biomass. The number of ramets and clonal propagules (corms) per pot was also recorded. Root morphological traits—including total length, surface area, volume, and average diameter—were assessed using the WinRHIZO image analysis system (Regent Instruments Inc., Québec City, QC, Canada).

Soil samples were collected from each pot and analyzed for a range of physicochemical properties. Soil pH and EC were measured as described in Section 2.2. Gravimetric water content was determined by drying soil at 105 °C. Nitrate nitrogen (NO_3^--N) and ammonium nitrogen (NH_4^+-N) were extracted with 2 mol·L^{-1} KCl and quantified using a continuous flow analyzer (AA3, Norderstedt Instrumental Analysis GmbH, Germany). Available phosphorus (AP) was extracted using 0.5 mol·L^{-1} $NaHCO_3$ and determined by the molybdenum blue colorimetric method. The potential nitrification rate (PNR) was evaluated via the chlorate inhibition technique, wherein soil samples were incubated with ammonium chloride and sodium chlorate. Accumulated nitrite (NO_2^--N) was quantified spectrophotometrically to estimate PNR. All chemical analyses were conducted following standard protocols described in the *Handbook of Soil Agricultural Chemistry Analysis* [32]. The surface sediments in the study area are predominantly composed of silt-sized particles ranging from 3.9 to 62.5 μm, characterized by an approximate water-holding capacity of 27%. Physicochemical analyses revealed that these sediments exhibit a mean pH of 8.42 ± 0.15, salinity of 0.36 ± 0.05 g/kg, and electrical conductivity (EC) of 96.7 μS/cm. The sediments also contain an organic carbon content of 5.48 ± 0.29 g/kg, with ammonium nitrogen (NH_4^+-N) and nitrate nitrogen (NO_3^--N) concentrations of 21.63 ± 0.70 mg/kg and 12.72 ± 0.58 mg/kg, respectively.

2.5. Statistical Analysis

The raw data were checked for normality, and natural-log or squareroot transformation was performed when necessary before analysis. One-way analysis of variance (ANOVA) was conducted to assess the effects of different biochar treatments on plant and soil parameters. Significant differences between treatment means were identified using Tukey's HSD post hoc test, with a significance threshold of $p < 0.05$. Pearson correlation

analysis was also performed to explore relationships between root morphological traits and soil nutrient availability. All statistical analyses were conducted in R version 4.2.2 [33].

3. Results

3.1. Effects of Spartina alterniflora-Derived Biochar on the Plant Traits of Scirpus mariqueter

As illustrated in Figure 1, the total and belowground biomass of *Scirpus mariqueter* exhibited significant responses ($p < 0.05$) to increasing concentrations of *Spartina alterniflora*-derived biochar, displaying a unimodal trend. A similar pattern was observed for aboveground biomass. Compared to CK, biochar additions at 0.5% and 1% increased aboveground biomass by 3.09% and 36.65%, and belowground biomass by 15.14% and 115.04%, respectively. The 1% biochar treatment significantly enhanced both total and belowground biomass ($p < 0.05$). In contrast, the 3% biochar application led to a marked decline in belowground biomass.

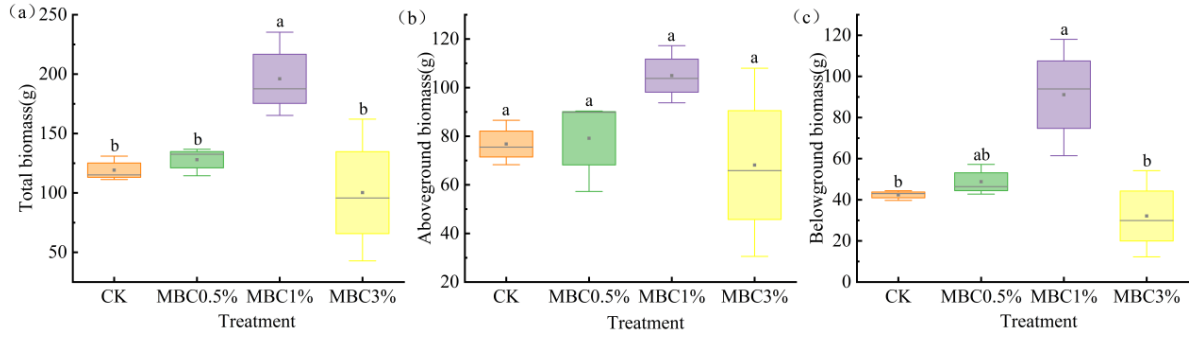


Figure 1. Effects of *Spartina alterniflora*-derived biochar on the biomass of *Scirpus mariqueter*: (**a**) total biomass, (**b**) aboveground biomass, and (**c**) belowground biomass. MBC0.5%, MBC1%, and MBC3% denote biochar application rates of 0.5%, 1%, and 3% (w/w), respectively, with control plots (CK) receiving no biochar amendment. Different lowercase letters indicate significant differences among treatments ($p < 0.05$).

In terms of vegetative growth, plant height increased significantly with rising concentrations of *Spartina alterniflora*-derived biochar (Figure 2a), indicating enhanced vegetative growth. In terms of reproductive traits, biochar addition had distinct effects on both asexual and sexual reproduction (Figure 2b–f). Among asexual traits, the number of ramets significantly decreased with increasing biochar concentration ($p < 0.05$; Figure 2b). The number of corms varied significantly among treatments ($p < 0.05$; Figure 2c), with increases of approximately 39.80% and 26.02% under the 0.5% and 3% treatments, respectively, compared to the CK. No significant difference was observed under the 1% treatment. Corm biomass did not differ significantly among treatments ($p > 0.05$; Figure 2d), although the 0.5% and 3% biochar additions resulted in increases of approximately 39.07% and 25.47% relative to the CK. Regarding sexual reproduction, both seed number and seed biomass varied significantly across biochar concentrations ($p < 0.05$; Figure 2e–f). Compared to CK, the 3% treatment significantly reduced both seed number and seed biomass ($p < 0.05$), while the 0.5% treatment had no significant effect. Notably, the 1% treatment significantly increased seed biomass ($p < 0.05$).

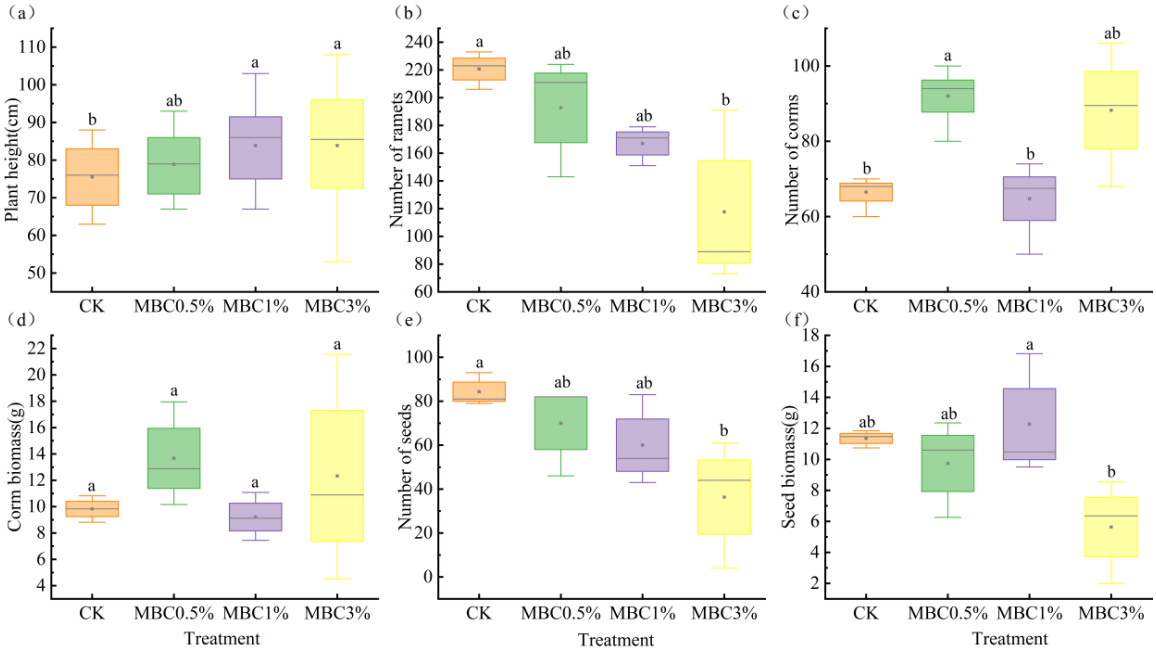


Figure 2. Effects of *Spartina alterniflora*-derived biochar on the vegetative and reproductive traits of *Scirpus mariqueter*: (**a**) plant height; (**b**) number of ramets; (**c**) number of corms; (**d**) corm biomass; (**e**) number of seeds; (**f**) seed biomass. Different lowercase letters indicate significant differences among treatments ($p < 0.05$).

The proportion of sexual reproductive biomass (seeds) relative to total plant biomass varied significantly among the *Spartina alterniflora*-derived biochar treatments ($p < 0.05$; Figure 3a), showing a clear decreasing trend with increasing biochar concentration. Compared to CK, this proportion declined by 21.54%, 41.18%, and 39.01% under the 0.5%, 1%, and 3% treatments, respectively, with the lowest value observed at the 1% level ($p < 0.05$). The proportion of asexual reproductive biomass (corms) also differed significantly among treatments ($p < 0.05$; Figure 3b). The 3% treatment exhibited the highest proportion, significantly exceeding those of the CK and 1% treatments, while the 1% treatment showed the lowest proportion among all groups ($p < 0.05$). In addition, the ratio of sexual to asexual reproductive biomass (seed/corm ratio) decreased significantly with increasing biochar concentration ($p < 0.05$; Figure 3c). Both the 0.5% and 3% treatments resulted in lower ratios compared to CK, with the 3% treatment displaying the lowest value, significantly lower than all other treatment groups.

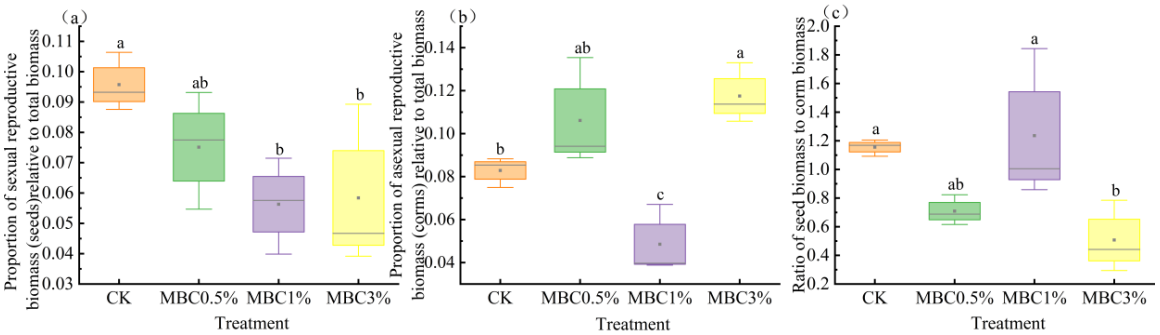


Figure 3. Effects of *Spartina alterniflora*-derived biochar on the reproductive allocation of *Scirpus mariqueter*: (**a**) proportion of seed biomass relative to total biomass; (**b**) proportion of corm biomass relative to total biomass; (**c**) ratio of seed biomass to corm biomass. Different lowercase letters indicate significant differences among treatments ($p < 0.05$).

3.2. Effects of *Spartina alterniflora*-Derived Biochar on Soil Physicochemical Properties

The application of *Spartina alterniflora*-derived biochar significantly influenced soil physicochemical properties in *Scirpus mariqueter* habitats ($p < 0.05$; Table 1). Soil moisture content increased progressively with higher biochar concentrations, reaching a maximum under the 3% treatment (12.54% higher than CK). Soil pH significantly increased under the 0.5% and 1% treatments but declined at the 3% level, while both EC and salinity exhibited nonlinear responses—initially decreasing and then increasing—with the highest values observed under the 3% treatment, where EC was 28.04% greater than CK. AP followed a similar pattern, increasing by 20.15% and 41.36% under the 1% and 3% treatments, respectively. Biochar addition also significantly enhanced soil nitrogen availability: NH_4^+-N peaked at the 0.5% level with a 26.84% increase, whereas NO_3^--N increased by 14.35% and 18.57% under the 1% and 3% treatments, respectively. Moreover, TC rose markedly with increasing biochar application, with the 0.5%, 1%, and 3% treatments showing increases of 10.94%, 14.24%, and 42.18%, respectively, compared to CK.

Table 1. Effects of *Spartina alterniflora*-derived biochar on soil physicochemical properties in *Scirpus mariqueter* habitats.

Treatment	CK	MBC0.5%	MBC1%	MBC3%
pH	7.67 ± 0.08 a	7.82 ± 0.03 a	7.75 ± 0.04 a	7.49 ± 0.01 b
Moisture (%)	46.48 ± 0.89 b	48.81 ± 0.87 ab	51.96 ± 0.98 a	52.31 ± 2.09 a
EC (μS/cm)	136.57 ± 9.03 b	121.20 ± 2.60 b	133.03 ± 7.79 b	174.87 ± 3.06 a
Salinity (g/kg)	0.27 ± 0.02 b	0.24 ± 0.01 b	0.27 ± 0.02 b	0.35 ± 0.01 a
AP (mg/kg)	84.40 ± 13.49 ab	83.88 ± 2.74 b	101.40 ± 3.02 ab	119.30 ± 1.95 a
NH_4^+-N (mg/kg)	26.16 ± 0.84 b	33.18 ± 3.13 a	30.39 ± 0.81 ab	30.86 ± 0.73 ab
NO_3^--N (mg/kg)	15.02 ± 0.57 c	15.69 ± 0.66 bc	17.17 ± 0.17 ab	17.81 ± 0.36 a
TC (g/kg)	53.89 ± 0.87 c	59.78 ± 1.60 b	61.56 ± 1.07 b	76.62 ± 2.17 a

Note: Abbreviations: EC, electrical conductivity; AP, available phosphorus; NH_4^+-N, ammonium nitrogen; NO_3^--N, nitrate nitrogen; TC, total carbon. Different lowercase letters indicate significant differences among treatments ($p < 0.05$).

3.3. Effects of *Spartina alterniflora*-Derived Biochar on Root Morphology of *Scirpus mariqueter*

The application of *Spartina alterniflora*-derived biochar significantly enhanced root development in *Scirpus mariqueter* ($p < 0.05$; Table 2). With increasing biochar concentration, root length, surface area, and volume displayed a unimodal (hump-shaped) response, peaking under the 1% treatment and subsequently declining. Compared to CK, the 1% biochar addition resulted in substantial increases in root length (135.84%), surface area (128.39%), and volume (82.26%) ($p < 0.05$). Root average diameter also varied significantly among treatments ($p < 0.05$), with the highest value observed under the 3% treatment—23.68% greater than CK—while the value under the 1% treatment was slightly lower than that of CK.

Table 2. Root morphological traits of *Scirpus mariqueter* in response to *Spartina alterniflora*-derived biochar application.

Treatments	Root Length (cm)	Root Surface Area (cm^2)	Root Volume (cm^3)	Root Avgrage Diameter (mm)
CK	101.02 ± 20.47 b	18.25 ± 3.14 b	0.26 ± 0.04 b	0.58 ± 0.02 b
MBC0.5%	108.13 ± 21.42 b	21.62 ± 3.20 b	0.35 ± 0.03 ab	0.65 ± 0.04 ab
MBC1%	238.25 ± 34.52 a	41.67 ± 3.68 a	0.48 ± 0.09 a	0.56 ± 0.03 b
MBC3%	133.40 ± 26.18 b	29.84 ± 5.09 ab	0.42 ± 0.06 ab	0.72 ± 0.02 a

Note: Values are presented as mean ± standard error. Different lowercase letters indicate significant differences among treatments ($p < 0.05$).

3.4. Correlation Analysis Among Plant Traits, Root Morphology, and Soil Properties

Correlation analysis revealed that most plant biomass traits were not significantly related to soil nutrients ($p > 0.05$), except for seed biomass, which was negatively correlated with TC ($p < 0.05$). Biomass traits showed positive correlations with root length and surface area ($p < 0.05$). Plant height was positively correlated with soil NO_3^--N, AP, EC, salinity, and TC ($r = 0.74$, $p < 0.01$), but negatively with seed biomass, ramet number, and pH ($p < 0.05$). Sexual traits were positively associated with ramet number, while seed number was negatively correlated with soil moisture ($p < 0.05$). Asexual traits showed weak correlations, though ramet number was positively correlated with pH and negatively with TC ($p < 0.05$).

4. Discussion

This study demonstrates that biochar derived from the invasive species *Spartina alterniflora* has significant, concentration-dependent effects on the growth, reproductive strategies, and root architecture of *Scirpus mariqueter*, while simultaneously altering the physicochemical properties of coastal wetland soils. These findings provide new insights into the use of biochar as a nature-based restoration tool, highlighting its potential to enhance native plant productivity and improve soil functioning in degraded tidal wetlands.

Among the tested treatments, moderate biochar application (1%) most effectively promoted plant growth, with total, shoot, and root biomass increasing by 64.53%, 36.65%, and 115.04%, respectively, relative to CK (Figure 1). This growth enhancement is likely driven by improved soil structure, increased nutrient retention, and enhanced rhizosphere conditions—consistent with previous studies indicating that biochar can enhance nutrient bioavailability and soil water-holding capacity [34,35]. Previous studies have shown that the abundant microporous structure of biochar enhances its capacity to adsorb and retain nutrient ions in the soil, thereby reducing nutrient leaching and improving plant nutrient use efficiency [36,37]. Moreover, biochar can indirectly promote nutrient uptake by modulating soil pH and electrical conductivity, which subsequently influences the composition and functional dynamics of rhizosphere microbial communities [38]. In contrast, the 3% biochar treatment negatively impacted plant biomass, particularly belowground, possibly due to elevated soil salinity and EC (Table 1), which can induce osmotic stress, restrict nutrient uptake, and inhibit root elongation [39,40]. Root morphological responses support this interpretation: the 1% treatment significantly improved root length, surface area, and volume, suggesting improved soil–root interactions, whereas the 3% treatment increased root diameter but reduced absorptive capacity, likely reflecting a stress-induced thickening response [41,42].

Biochar application also influenced reproductive allocation, shifting the balance between sexual and asexual strategies in *Scirpus mariqueter* (Figures 2 and 3). While low biochar levels promoted the development of clonal organs (corms), higher concentrations reduced seed production and sexual reproductive biomass, indicating a trade-off potentially driven by nutrient enrichment and salinity stress. This pattern aligns with previous findings that nutrient-rich conditions tend to favor vegetative propagation, whereas increased salinity and EC can reduce investment in sexual reproduction [2,43]. Further analysis suggests that biochar may influence plant reproductive strategies through multiple interacting mechanisms. First, due to its high specific surface area and porous structure, biochar can adsorb nutrients and improve soil physical properties, thereby enhancing soil water and nutrient retention capacity [44,45]. This, in turn, facilitates more efficient acquisition of belowground resources and promotes the development of roots and corms. Second, biochar has been shown to regulate soil pH and salinity levels [46,47], which may help alleviate the inhibitory effects of salt stress on sexual reproduction. However, at

higher application rates, biochar may negatively affect plant growth and seed formation by disrupting rhizosphere microbial communities or inducing ion toxicity [48]. Additionally, biochar may influence reproductive allocation by modulating plant hormone levels, such as auxin and abscisic acid [49]. Correlation analysis further supports this mechanism: root volume was positively associated with NH_4^+-N and NO_3^--N, indicating a key role of nitrogen in promoting root development and clonal expansion (Figure 4). However, the weak or inconsistent correlations between asexual reproductive traits and soil variables suggest that other ecological factors—such as light availability, hydrological conditions, and biotic interactions—may also regulate reproductive plasticity, highlighting the need for further field-based research [50].

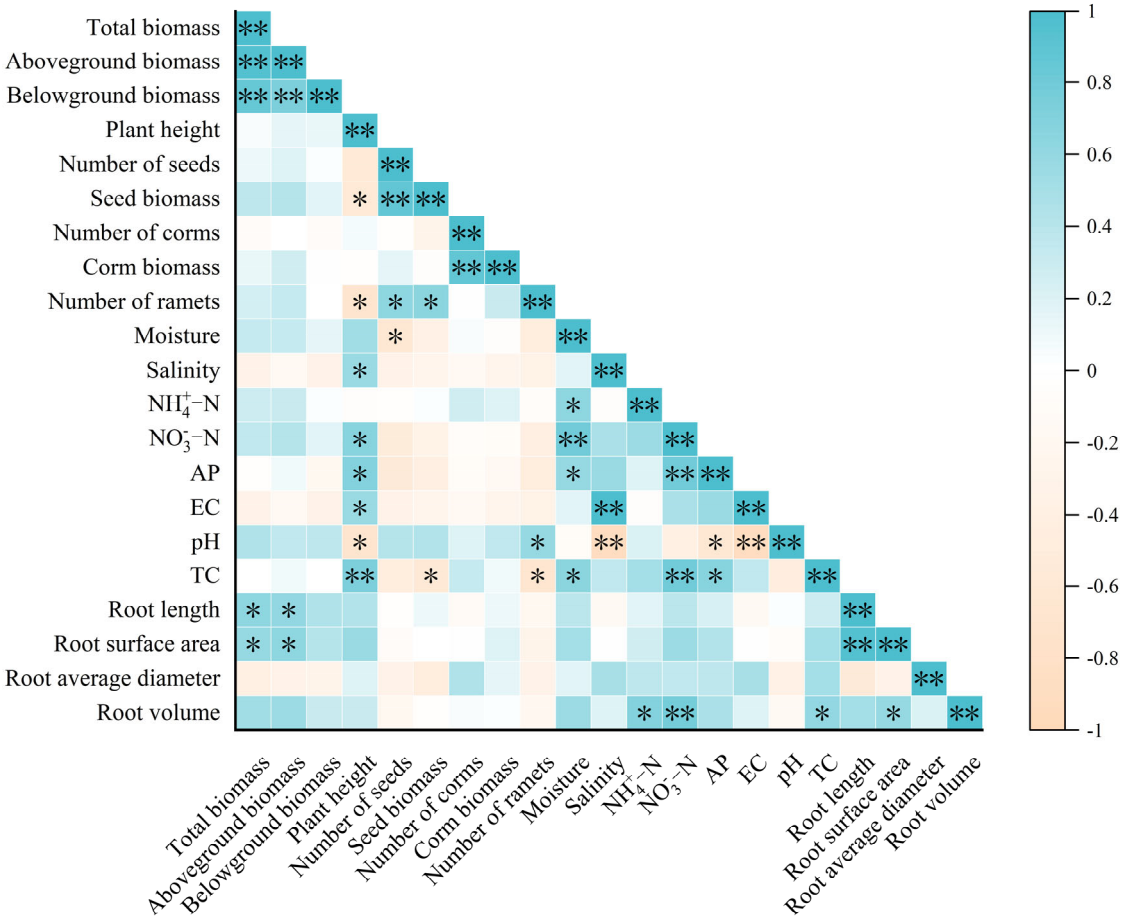


Figure 4. Spearman's correlation heatmap between plant traits of *Scirpus mariqueter* and soil nutrient variables. Colors indicate the strength of correlation coefficients. Asterisks indicate levels of statistical significance (* $p < 0.05$; ** $p < 0.01$).

The observed improvements in soil properties underscore biochar's multifaceted role in enhancing ecosystem functions (Table 1). In particular, increased soil moisture, available nutrients (AP, TC, NH_4^+-N, NO_3^--N), and potential nitrification under the 1% treatment suggest enhanced microbial activity and nutrient cycling, which are critical for sustaining plant productivity and facilitating soil carbon input [51,52]. In addition, soluble organic compounds and leachates released from biochar can serve as readily available carbon sources for soil microorganisms, thereby stimulating microbial metabolic activity and accelerating the mineralization of nitrogen and phosphorus, as well as the decomposition of organic matter [53,54]. These processes collectively contribute to improved nutrient availability and uptake by plants. Furthermore, biochar may indirectly influence the composition and functional gene expression of soil microbial communities. For example, it

has been shown to increase the relative abundance of ammonia-oxidizing bacteria (AOB) and denitrifying bacteria, thereby enhancing soil nitrification potential and nitrogen use efficiency [49,55]. In coastal wetlands—key blue carbon ecosystems—belowground biomass is closely linked to carbon sequestration potential [4,8]. Thus, moderate biochar addition could simultaneously support vegetation recovery and long-term carbon storage.

However, the accumulation of salts and reduction in pH observed under the 3% treatment highlight potential ecological risks associated with high biochar dosages, such as shifts in microbial community composition and inhibited plant performance [1,43]. Therefore, while this study supports the use of *Spartina alterniflora*-derived biochar as a viable strategy for wetland restoration, its application should be carefully tailored to site-specific conditions. Consideration of appropriate dosage thresholds, hydrological context, and species-specific tolerance is essential to maximize ecological benefits while minimizing unintended consequences.

Invasive weeds have recently garnered increasing attention as promising feedstocks for biochar production due to their high biomass availability, elevated carbon content, and potential to improve soil fertility and structure. A growing body of research has demonstrated that, when applied at appropriate rates, weed-derived biochars can significantly enhance soil physicochemical properties and promote plant growth [24,56]. Collectively, these findings highlight the potential of weed-derived biochar as a sustainable tool for soil remediation and nutrient management.

While earlier studies have primarily emphasized the general benefits of invasive plant-derived biochar for soil improvement, the novelty of the present study lies in its focus on the biochar's role in enhancing both the growth and reproductive allocation of *Scirpus mariqueter*, a native coastal wetland species. By elucidating the relationships between soil nutrient dynamics and shifts in plant reproductive strategies across a gradient of biochar application rates, this study contributes new insights into the ecological functions of biochar in coastal wetland restoration. Furthermore, the findings underscore the "dual value" of invasive weeds: mitigating ecological threats through biomass valorization, while simultaneously supporting native species recovery and advancing blue carbon management strategies.

However, a critical limitation of this study is the lack of investigation into the dynamics of labile carbon fractions leached from invasive plant-derived biochar and their potential priming effects on the mineralization of native soil organic matter (SOM). Such processes may increase dissolved organic carbon levels in adjacent water bodies, with potential downstream impacts on aquatic ecosystem structure and function [57]. Future research should therefore aim to quantify carbon leaching and associated priming effects following biochar application in coastal wetlands. A mechanistic understanding of these pathways will be essential for assessing ecological risks and developing optimized biochar application strategies that maximize ecological benefits while minimizing unintended environmental consequences.

5. Conclusions

This study provides empirical evidence that biochar derived from the invasive plant *Spartina alterniflora* can significantly enhance the growth performance, reproductive traits, and root morphology of the native halophyte *Scirpus mariqueter*, while concurrently improving soil moisture, nutrient availability, and nitrification activity in coastal wetland sediments. Notably, a moderate biochar application rate (1%) was most effective in maximizing plant biomass and reproductive efficiency, indicating an optimal threshold for balancing vegetation growth and soil improvement. In contrast, excessive application (3%) increased soil salinity and electrical conductivity, leading to suppressed plant develop-

ment and altered reproductive allocation, thereby emphasizing the critical importance of dosage control in ecological applications. These findings highlight the potential of *Spartina alterniflora*-derived biochar as a sustainable and circular resource for coastal wetland restoration, offering dual benefits in terms of invasive biomass utilization and enhanced blue carbon sequestration. Nevertheless, the negative impacts observed at higher concentrations underscore the need for careful ecological risk assessment. Future research should incorporate long-term field trials and integrate soil microbial community analyses to better elucidate the mechanisms and ecological thresholds governing biochar performance in tidal wetland ecosystems.

Author Contributions: Project administration, N.L.; conceptualization, N.L. and Y.T.; investigation, J.G., P.J. and J.L.; methodology, Y.T.; data curation, Y.T.; formal analysis, Y.T. and M.W.; visualization, Y.T.; writing—original draft, Y.T.; writing—review and editing, S.J., L.Z. and X.S., N.L. and X.S. contributed equally to this work. All authors have read and agreed to the published version of the manuscript.

Funding: This study was supported by the Pioneer and Leading Goose R&D Program of Zhejiang Province (Grant No. 2024C02002); the Zhejiang Province Commonwealth Projects (Grant No. LQ23C030003); the Cooperation Program between Zhejiang Province and the Chinese Academy of Forestry (Grant No. 2023SY11); the Special Fund for Basic Scientific Research Operations of Central Public Welfare Research Institutes (Grant No. CAFYBB2024MA029); the Zhejiang Provincial Science and Technology Program (Grant No. 2023C03120); the Pioneer and Leading Goose R&D Program of Zhejiang Province (Grant Nos. 2025C02050 and 2025C02230); and the National Key Research and Development Program of China (Grant No. 2023YFE0101700).

Institutional Review Board Statement: Not applicable.

Data Availability Statement: The datasets used and analyzed during the current study are available from the corresponding author.

Acknowledgments: We express our sincere gratitude to Xiaohong Zhu from Wetland Ecosystem Research Station of Hangzhou Bay for his invaluable assistance and insightful suggestions during the study.

Conflicts of Interest: The authors declare no conflicts of interest.

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