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# Seasonal soil-plant nitrogen dynamics of a cordgrass salt marsh in response to coastal embankments in Eastern China

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The effects of coastal embankments on nitrogen (N) cycling in the *Spartina alterniflora* salt marsh have been extensively reported. However, it remains unclear effects of the embankment on the sizes of diverse N subpools in the plant-soil subsystems year-round. This study examined seasonal changes in various N subpools of plant subsystems; soil subsystems [e.g., soil organic N (SON), recalcitrant organic N (RON), labile organic N (LON), dissolved organic N (DON), ammonium N(NH<sub>4</sub><sup>+</sup>N), and nitrate N(NO<sub>3</sub><sup>-</sup>N)]; N mineralization [e.g., soil net ammonification (R<sub>A</sub>) and nitrification (R<sub>N</sub>) rate]; and immobilization [e.g., microbial biomass N (MBN)] in embanked and adjacent *S. alterniflora* natural salt marshes on the coast of Eastern China. The embankment significantly reduced the litter N storage by 62.7–71.8% over the four seasons and decreased the root N storage by 53.0% during winter. The SON, LON, RON, and N H<sub>4</sub><sup>+</sup>N concentrations declined significantly by 43.0–60.2%, 35.8–64.8%, 44.9–59.0%, and 20.8–42.2%, respectively, over the four seasons following the embankment construction. Furthermore, the embankment dramatically reduced the DON concentrations by 21.9% in spring, 14.6% in summer, and 10.4% in winter, while notably diminishing the NO<sub>3</sub><sup>-</sup>N concentrations by 33.4% in autumn and 44.9% in winter, and the R<sub>A</sub> and R<sub>N</sub> in spring and summer. However, the embankment clearly increased the MBN concentrations during summer and autumn, the NO<sub>3</sub><sup>-</sup>N concentrations in spring, and the R<sub>A</sub> and R<sub>N</sub> in winter at different levels. Due to the decreased soil N inputs from plants, the embankment decreased the organic and inorganic N subpools every season to varying degrees, except for the NO<sub>3</sub><sup>-</sup>N concentration in spring. We suggest that the decreased soil salinity following embankment establishment might increase the uptake of ions by microbes, while stimulating the production of MBN. Ultimately, the NO<sub>3</sub><sup>-</sup>N and DON were two vital N sources for *S. alterniflora*, and plants absorbed N from the soil to promote their biomass, as well as N concentration and storage. This study is conducive toward understanding the mechanisms behind the effects of coastal

embankments on the N transfer among various N subpools in the plant and soil systems.

#### KEYWORDS

coastal reclamation, soil nitrogen subpool, nitrogen cycling, plant nitrogen subpool, soil microbial biomass

## Introduction

Coastal embankments function to hold seawater back from salt marshes. Many countries spanning Europe, North America, and East Asia have established coastal embankments to promote regional economic development (Iost et al., 2007; Kirwan and Megonigal, 2013), satisfy local demands for farming and housing (Barbier et al., 2011), and control invasive plants (An et al., 2007). More than 60% of coastline is enclosed by embankments in China (Ma et al., 2014), which has led to significant alterations in local biogeochemical cycles (e.g., nitrogen (N) cycling) (Yang et al., 2016; van de Broek et al., 2019; Zhou and Bi, 2020; Feng et al., 2022). Biogeochemical cycling is complex and can be influenced by myriad factors (Purvaja et al., 2008; Aufdenkampe et al., 2011; Lin and Lin, 2022). Although the impacts of coastal embankments on biogeochemical cycling have been extensively reported (Yang et al., 2016; van de Broek et al., 2019; Feng et al., 2022), few investigation has explored the seasonal dynamics of N pools following the establishment of embankments in salt marshes.

Seasonality may directly affect N cycling *via* soil moisture and temperature, or indirectly through modified plant productivity and the seasonal patterns of organic matter release (Wuest, 2015; Zhao et al., 2016; Evangelou et al., 2021). For instance, the accumulation of soil organic N is generally positively related to seasonal variations in soil moisture, which influences soil oxygen levels that affect the rate at which debris is

decomposed by microorganisms (Huang et al., 2013; Zhao et al., 2016). However, higher salinity levels can inhibit the activities of soil microorganisms during N cycling (Gao et al., 2012; Zhao et al., 2016). Moreover, seasonal SON in coastal ecosystems has positive correlations with the quality and quantity of plant residues (e.g., plant litter biomass), which exhibit seasonal variations (Ake-Castillo et al., 2006; Elsey-Quirk et al., 2011). Generally, the decomposition rates of plant residues are positively correlated with the average annual temperature, precipitation, etc. (Ake-Castillo et al., 2006; Battle and Golladay, 2007; Abu Hena et al., 2015), which also ultimately impact the seasonal SON. Several earlier studies also have demonstrated that higher net N mineralization rates in the soil and the N uptake of plants always occur in warmer environments, which has combined effects on the magnitudes of soil inorganic N pools (Augustine et al., 2014; Hu et al., 2015; Sanders-DeMott et al., 2018). Similarly, soil-residing inorganic N pools can be affected by the minimal activities of plants and microorganisms during autumn and/or winter (Urakawa et al., 2014; Sanders-DeMott et al., 2018). Soil microbial biomass N (MBN) comprises the mass of the living components of soil organic N, wherein soil microorganisms absorb both dissolved organic N (DON) and inorganic N (e.g., ammonium ( $\text{NH}_4^+$ ) and nitrate ( $\text{NO}_3^-$ )) and transform them to MBN (Wang et al., 2019; Evangelou et al., 2021). As recently reported that the highest concentrations of MBN are observed during the warmer season (e.g., spring and/or autumn) in coastal ecosystems (Liu et al., 2019; Chen et al., 2022). Therefore, the seasonality has important effects on the plant-soil N dynamics in temperate coastal regions (Urakawa et al., 2014; Sanders-DeMott et al., 2018; Wang et al., 2018) through dynamic N fixation (Dovrat and Sheffer, 2019), plant uptake (Socci and Templer, 2011), and N mineralization (Hu et al., 2015; Huang et al., 2021); and determining effects of coastal embankments on various N pools in different seasons may improve our understanding of how these embankments impact N pools or N cycling in salt marshes.

Jiangsu Province is home to the largest coastal wetland area (4570 km<sup>2</sup>) and longest stretches of coastal embankments (954 km) in China (Zhang et al., 2006; Zhang et al., 2013; Cui et al., 2018). The exotic *Spartina alterniflora* Loisel (*S. alterniflora*) is the dominant plant along Chinese coasts, which was introduced from North America in 1979 (Xu and Zhuo,

**Abbreviations:** ALB, Aboveground living biomass; ANC, Aboveground living N concentration; ANS, Aboveground living N storage; ANOVA, Analysis of variance; BPlant, biomass per centiare; C<sub>N</sub>Plant, N concentration; DON, Dissolved organic N; ESA, Embanked *Spartina alterniflora* salt marshes; LB, Litter biomass; LNC, Litter N concentration; LNS, Litter N storage; LON, Labile organic N; MBC, Microbial biomass carbon; MBN, Microbial biomass N; N, Nitrogen;  $\text{NH}_4^+$  - N, Ammonium N; NMDS, Non-metric Multi-Dimensional Scaling;  $\text{NO}_3^-$  - N, Nitrate N;  $\text{NO}_2^-$  - N, Nitrite N; NSA Natural *Spartina alterniflora* salt marshes; PE, Polyethylene; R<sub>A</sub> Soil net, ammonification rate; RB, Root biomass; R<sub>N</sub> Soil net, nitrification rate; RNC, Root N concentration; RNS, Root N storage; RMSEA, Root-mean-square error of approximation; RON, Recalcitrant organic N; S<sub>N</sub> Plant, N storage; SON Total; soil organic N; SEM, Structural equation modelling.

1985; An et al., 2007) and over the last few decades has expanded rapidly across salt marshes (An et al., 2007; Wan et al., 2009). A growing number of studies have focused on the ecological management of *S. alterniflora* (An et al., 2007; Patten et al., 2017), with coastal embankments being one of the more common approaches at present (An et al., 2007; Ma et al., 2014).

Our previous studies revealed that embankments significantly decreased the biomass and N storage capacities of plants, soil N pools, and soil microbial diversity, and altered the compositions of soil microbial communities in *S. alterniflora* salt marshes during the growing season (Yang et al., 2016; Feng et al., 2017; Feng et al., 2022). However, to the best of our knowledge, there exists very limited knowledge regarding the seasonal dynamics of N pools in natural salt marshes and those with embankments. Furthermore, seasonal variations in salt marshes following the development of coastal embankments should not be disregarded, as they may have additional deleterious effects on soil N dynamics.

Consequently, we hypothesized that embankments may reduce variant N subpools in the soil and plant subsystems in *S. alterniflora* salt marshes year-round. For this study, to verify our hypothesis, we compared various soil N subpools, plant N subpools, microorganismal growth (e.g., microbial biomass carbon (MBC) and MBN), soil N transformation rates (e.g., N immobilization and mineralization), and physiochemical soil properties in both embanked and adjoining natural *S. alterniflora*-dominated salt marshes in April, July, October 2017, and January 2018. The primary objectives of this study were to quantify and identify the (1) effects of the embankment on the sizes of various N subpools in the *S. alterniflora* salt marsh in four seasons, and (2) how the embankment influenced the N transfer among various N subpools in plant and soil subsystems in plant and soil subsystems. Ultimately, this study sought to provide a theoretical basis for the control and rational utilization of *S. alterniflora*, particularly in the coastal ecosystem where the primary productivity is conventionally thought to be limited by N (Vitousek et al., 1997).

## Materials and methods

### Site description

The field work for this study was conducted in the core region of the Dafeng Milu National Nature Reserve (32°59'N-33°03'N, 120°47'E-120°53'E), on the Yellow Sea coast of Jiangsu Province, China (Figure 1). This Reserve was established in 1986 and is listed as part of the World Natural Heritage in 2019, as it plays a significant role in international biodiversity conservation. It is situated such that it encompasses the transition of warm temperate and northern subtropical zones, which are primarily impacted by oceanic and continental climates (Cui et al., 2018). According to the report of China Meteorological Administration, the mean monthly temperatures were 13.1°C in April, 26.7°C in July, 16.5°C in October, and 1.6°C in January; the mean monthly precipitations

were 55.2 mm in April, 251.3 mm in July, 54.1 mm in October, and 33.9 mm in January; the radiations per unit area were 135 kw·m<sup>-2</sup> in April, 150 kw·m<sup>-2</sup> in July, 98 kw·m<sup>-2</sup> in October, and 70 kw·m<sup>-2</sup> in January. A regular semidiurnal tide occurs along the coastal area, with an annual average tidal range of about 3 m (Ren, 1986; Li et al., 2018).

The coastal embankments of this region were established in 2011, with a typical length, thickness, and height of 2400 m, 2 m, and 2 m, respectively. Thus, both seawater and river water are prevented from entering the embanked range. The natural and embanked ranges have not been subjected to anthropogenic activities or other disturbances (Yang et al., 2016).

### Field sample collection

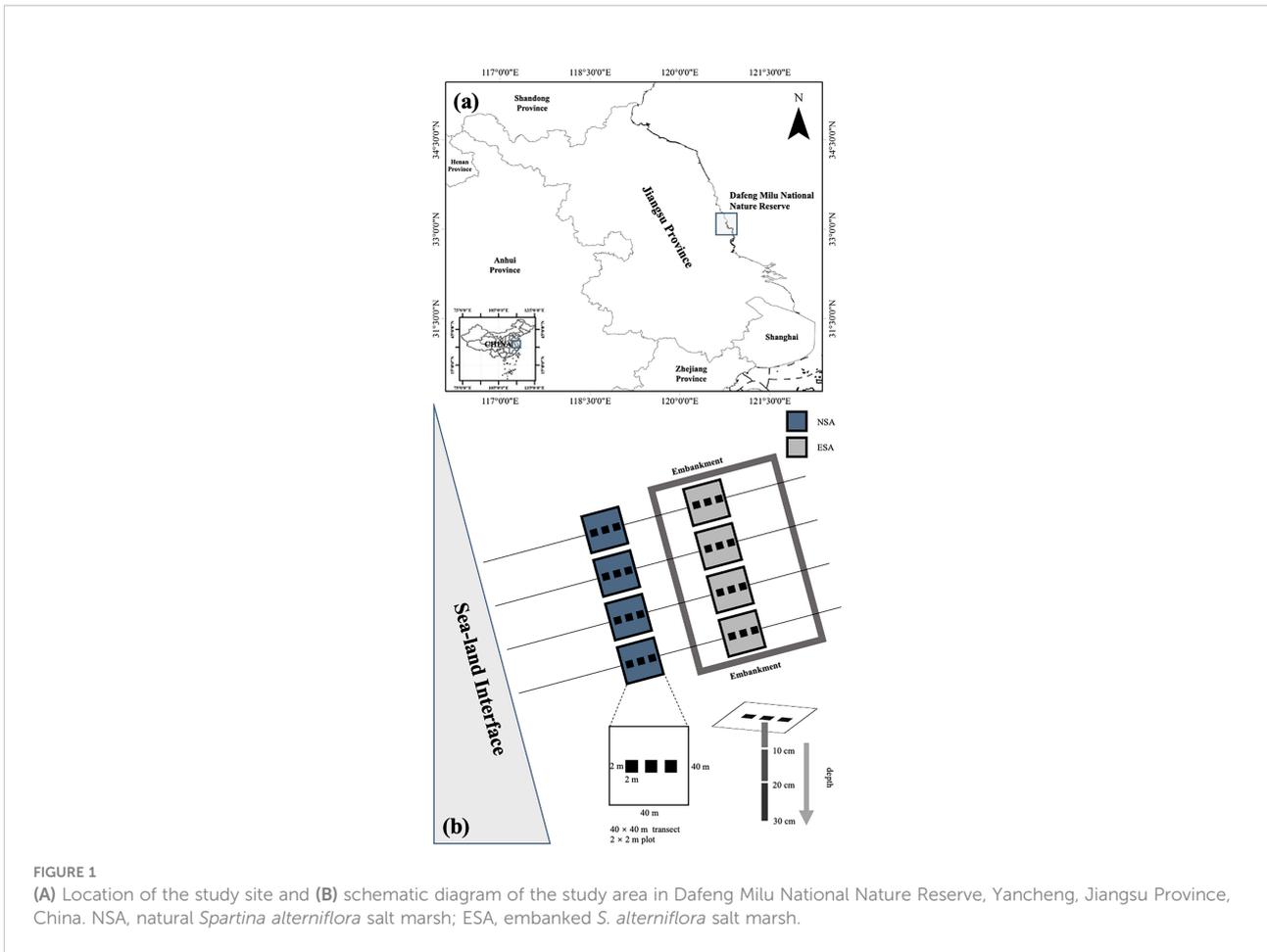
In spring (April 2017), summer (July 2017), autumn (October 2017), and winter (January 2018), four parallel transects (40 × 40 m) were established in the natural and embanked *S. alterniflora* salt marshes (Figure 1), and three plots (2 × 2 m) in each transect were randomly selected. Three soil core samples (0-10 cm, 10-20 cm, and 20-30 cm depths) were randomly extracted from each plot, whereafter core samples from the same depths and plots were evenly mixed as the final soil samples.

Briefly, 96 soil samples (four replicates × three depths × two treatments × four seasons) were obtained. Following the removal of all belowground plant components, the soil samples were transferred to the laboratory and divided into three subsamples. The first subsample was employed to measure the soil moisture, whereas the second was air-dried and sifted through a 1-mm sieve, which was used to determine the soil pH, salinity, SOC, and SON. The third fresh subsample was sifted through a 2-mm sieve and stored at 4°C, which was used to quantify the DON, MBC, MBN, NH<sub>4</sub><sup>+</sup> - N and NO<sub>3</sub><sup>-</sup> - N concentrations.

The soil net ammonification (R<sub>A</sub>) and nitrification (R<sub>N</sub>) rate were quantified using the closed-top PE (polyethylene) tube incubation technique, which was based on the sequential soil coring of the undisturbed soil and *in situ* exposure (Raison et al., 1987). Eight PE pipes (Ø5 cm x 30 cm long) per sample were vertically inserted into the soil at random, after which they were carefully extracted. Four PE pipes were transferred to the laboratory for the quantification of the NH<sub>4</sub><sup>+</sup> - N and NO<sub>3</sub><sup>-</sup> - N concentrations. The other four were buried *in situ* for cultivation to determine the NH<sub>4</sub><sup>+</sup> - N and NO<sub>3</sub><sup>-</sup> - N concentrations after 30 days, where their tops and bottoms were wrapped with plastic film and gauze, respectively. Furthermore, four quadrats (50 × 50 cm) were established in each transect for the acquisition of plant tissues, including leaves, stems, litter, and roots.

### Laboratory analyses

The leaves, stems, and litter were separated, whereas the roots were collected by sifting through a 100-mm sieve, which



was used to remove any clods and stones. All *S. alterniflora* tissues were thoroughly rinsed under running water (Yang et al., 2016). Each type of tissue biomass was oven-dried at 65°C, and the N concentration was determined using an Elementar Vario Micro CHNS analyzer (Elementar Analysen system GmbH, Germany). The tissue N storage for each plant was computed using the following formula:

$$S_N = C_N \times B \tag{1}$$

where  $S_N$  is the plant N storage,  $C_N$  is the plant N concentration, and  $B$  is the plant biomass per centiare.

The first fresh soil subsample was used to determine the soil bulk density (BD), pH, salinity, and moisture according to methods that reported by Slavich and Petterson (1990) and Yang et al. (2016).

The recalcitrant organic N (RON) was processed using the acid hydrolysis method (Rovira and Vallejo, 2002; Yang et al., 2016). The concentrations of SON and RON were measured using an Elementar Vario Micro CHNS analyser (Elementar Analysen system GmbH, Germany), whereas the labile organic N (LON) was computed using the following formula.

$$LON = SON - RON \tag{2}$$

Additionally, DON was determined following the procedure of Jones et al. (2004). The MBC and MBN concentrations were determined following the chloroform fumigation-extraction method (Brookes et al., 1985).

A mixture of 2.5 g of fresh soil samples and 25 mL of 2 M KCl (1:10 w/v soil:solution) were placed into 50 mL PP (polypropylene) bottles and shaken at 200 rpm for 60 min using a reciprocating shaker. Subsequently, the supernatant was employed to quantify the concentrations of  $NH_4^+ - N$ ,  $NO_2^- - N$  and  $NO_3^- - N$  with an AQ2+ Automated Discrete Analyser (SEAL, Britain, shown after the determination of  $R_A$  and  $R_N$ :

$$R_A = \frac{(NH_4^+ - N_{i+1}) - (NH_4^+ - N_i)}{t_{i+1} - t_i} \tag{3}$$

$$R_N = \frac{(NO_3^- - N_{i+1} + NO_2^- - N_{i+1}) (NO_3^- - N_{i+1} + NO_2^- - N_{i+1})}{t_{i+1} - t_i} \tag{4}$$

Where  $t_i$  and  $t_{i+1}$  are the incubation start and end times (d), respectively;  $\text{NH}_4^+ - \text{N}_i$  and  $\text{NH}_4^+ - \text{N}_{i+1}$  are the soil  $\text{NH}_4^+ - \text{N}$  concentrations (mg/kg) at the onset and conclusion of incubation, respectively;  $\text{NO}_2 - \text{N}_i$  and  $\text{NO}_2 - \text{N}_{i+1}$  are the soil  $\text{NO}_2 - \text{N}$  concentrations (mg/kg) at the start and end of incubation, respectively;  $\text{NO}_3^- - \text{N}_i$  and  $\text{NO}_3^- - \text{N}_{i+1}$  are the soil  $\text{NO}_3^- - \text{N}$  concentrations (mg/kg) at the beginning and end of incubation, respectively.

## Statistical analyses

We employed one-way analysis of variance (ANOVA) to (1) verify the impacts of the embankment on the concentrations of SON, DON, LON, RON,  $\text{NH}_4^+ - \text{N}$ ,  $\text{NO}_3^- - \text{N}$ , MBC, MBN,  $R_A$ , and  $R_N$ , as well as the biomass of aboveground living (ALB), litter (LB), and root (RB) tissues and N storage of aboveground living (ALNS), litter (LNS), and root (RNS) tissues for the different seasons; (2) confirmed the seasonal variations in these indices for the natural and embanked salt marshes; (3) seasonal plant and soil N subpools were studied with a NMDS (Non-metric Multi-Dimensional Scaling); (4) interactions of SON with LNS and RNS in the natural and embanked salt marshes were tested by using linear models. Besides, Multi-way ANOVA was employed to examine the impacts of embankment and season, as well as their interactive effects on the various N subpools in plant and soil subsystems. All above analyses were performed using R software (R Studio Inc., Massachusetts, USA).

We analyzed the relationships between plant biomass and N storage, various soil N fractions, MBC, MBN, and assorted mineralization rates for both natural and embanked *S. alterniflora* by using Pearson's correlation analysis (Figure S1). Furthermore, structural equation modelling (SEM) was utilized to test the multivariate relationships between the direct effects of the coastal embankment and indirect impacts of parameters during the different seasons related to soil organic and inorganic N, MBC, MBN,  $R_A$ , and  $R_N$ , which was based on a conceptual *a priori* model (Figure S2). Using the maximum likelihood for parameter estimation (Boldea and Magnus, 2009), the best fitting model was selected through the sequential removal of nonsignificant coefficients ( $p < 0.05$ ). We employed a chi-squared test ( $\chi^2$ ) and the root-mean-square error of approximation (RMSEA; Schermelleh-Engel et al., 2003) for evaluating the model. The SEM analysis was implemented using AMOS 22.0 software (IBM, SPSS, New York).

## Results

### Plant biomass and N allocation

The embankment significantly decreased the ALB, LB, ALNS, and LNS of *S. alterniflora* throughout the year, ranging

from 47.9% to 70.3%, 66.5% to 76.4%, 52.7% to 69.5%, and 62.7% to 71.8%, respectively ( $p < 0.05$ ; Figure 2). Further, they reduced the RB by 57.9% and 67.7% in autumn and winter, respectively, as well as the RNS by 53.0% in winter ( $p < 0.05$ ; Figure 2). Conversely, the embankment increased the ALNC remarkably by 24.8% in spring and the LNC by 20.2% in autumn, as well as the RNC by 49.7% and 80.8% in summer and autumn, respectively ( $p < 0.05$ ; Figure 2). Additionally, the maximum values of RB, RNS, and ALNC occurred in spring, and the peaks of AB and ANS appeared in autumn for both the natural and embanked salt marshes ( $p < 0.05$ ; Figure 2). The values of LNS and LB in spring and winter were remarkably higher than those in summer and autumn for both the natural and embanked salt marshes ( $p < 0.05$ ). The LNC values in both the natural and embanked salt marshes were the lowest during winter, with the lowest RNC value in the natural salt marsh appearing in autumn ( $p < 0.05$ ). However, there were no significant differences in the RNC value in the embanked salt marsh across all seasons ( $p \geq 0.05$ , Figure 2).

### Soil N subpools

In the soil organic N subpool, there were significant decreases in the concentrations of SON, LON, and RON in the embanked salt marsh, which ranged from 43.0% to 60.2%, 35.8% to 64.8%, and 44.9% to 59.0%, respectively, over the four seasons ( $p < 0.001$ ; Figure 3). In contrast to those in the natural salt marsh, the concentrations of DON in the embanked salt marsh decreased significantly by 21.9%, 14.6%, and 10.4% in spring, summer, and winter, respectively ( $p < 0.05$ ; Figure 3).

Negligible seasonal variations in the SON concentration values were observed in the natural salt marsh ( $p \geq 0.05$ ; Figure 3), with the exception of the highest being observed in spring for the embanked salt marsh ( $p < 0.05$ ; Figure 3). The maximum LON concentrations were observed in spring for both the natural and embanked salt marshes ( $p < 0.05$ ), but there is no difference in the LON concentrations between spring and winter in the natural salt marshes ( $p \geq 0.05$ ; Figure 3). The minimum concentration of RON was seen in spring for the natural salt marsh ( $p < 0.05$ ; Figure 3), while there were no significant seasonal changes in the RON concentrations in the embanked salt marsh ( $p \geq 0.05$ ; Figure 3). The lowest DON concentrations were observed in autumn for both the natural and embanked salt marshes (Figure 3).

For the soil inorganic N subpool, the effects of the embankment significantly influenced the soil  $\text{NH}_4^+ - \text{N}$  (Table 1). The embankment significantly decreased the soil  $\text{NH}_4^+ - \text{N}$  concentrations (20.8 – 42.2%) through spring, summer, autumn, and winter ( $p < 0.05$ ; Figure 3). The embankment also reduced the soil  $\text{NO}_3^- - \text{N}$  concentrations in autumn and winter by 33.4% and 44.9%, respectively, while they significantly increased the soil  $\text{NO}_3^- - \text{N}$  concentration by 132.6% in spring ( $p < 0.05$ ;

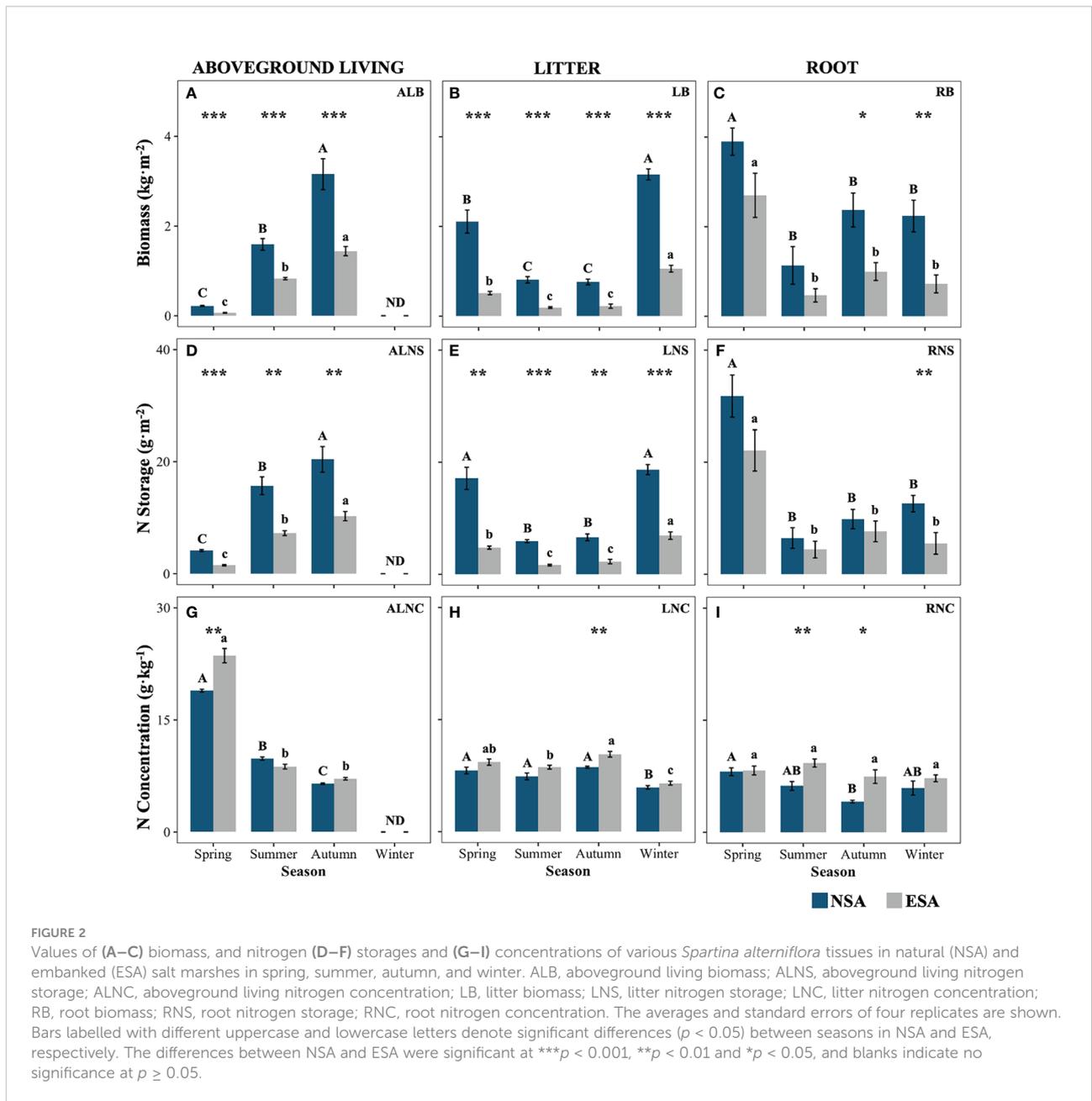


Figure 3). Moreover, the peak concentrations of soil  $\text{NH}_4^+ - \text{N}$  and  $\text{NO}_3^- - \text{N}$  were observed in autumn for both the natural and embanked salt marshes (Figure 3).

### Growth, N immobilization, and mineralization of microorganisms

The soil MBC concentration was significantly reduced by 52.1% in winter with the embankment, whereas on the contrary the soil MBN concentration significantly increased in summer and autumn by 189.2% and 200.8%, respectively ( $p < 0.05$ ; Figure 4). The peak

values of both the soil MBC and MBN concentrations were observed in winter for the natural salt marsh, whereas there were insignificant seasonal variations in the MBC and MBN following the establishment of the embankment ( $p < 0.05$ ; Figure 4).

Furthermore, both the  $R_A$  and  $R_N$  were remarkably reduced in spring and summer, while they were significantly increased in autumn following embankment development ( $p < 0.01$ ; Figure 4). The lowest  $R_A$  values ( $< 0 \text{ mg}\cdot\text{kg}^{-1}\cdot\text{d}^{-1}$ ) were observed in autumn, while they peaked in summer for both the natural and embanked salt marshes (Figure 4). The highest and lowest  $R_N$  values ( $p < 0.05$ ) were observed in spring and autumn, respectively, in the natural salt marsh, while the highest and lowest  $R_N$  values were

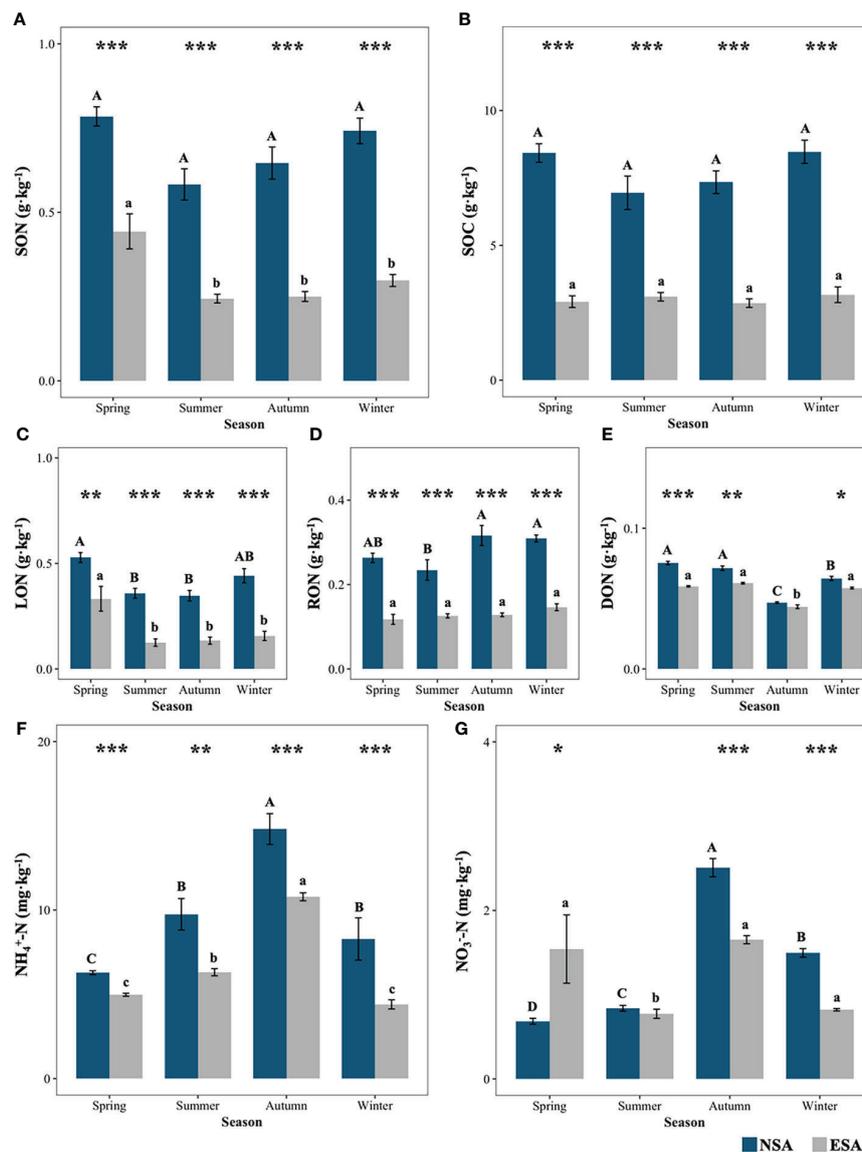


FIGURE 3

Values of (A) total soil organic nitrogen (SON), (B) total soil organic carbon (SOC), (C) labile organic nitrogen (LON), (D) recalcitrant organic nitrogen (RON), (E) dissolved organic nitrogen (DON), (F) ammonia nitrogen ( $\text{NH}_4^+\text{-N}$ ), and (G) nitrite nitrogen ( $\text{NO}_3^-\text{-N}$ ) in natural (NSA) and embanked (ESA) *Spartina alterniflora* salt marshes in spring, summer, autumn, and winter. The averages and standard errors of four replicates are shown. Bars labelled with different uppercase and lowercase letters denote significant differences ( $p < 0.05$ ) between seasons in NSA and ESA, respectively. The differences between NSA and ESA were significant at \*\*\* $p < 0.001$ , \*\* $p < 0.01$  and \* $p < 0.05$ , and blanks indicate no significance at  $p \geq 0.05$ .

observed in autumn and spring, respectively, in the embanked salt marsh (Figure 4).

## Physicochemical soil properties

The soil moisture and salinity values in the embanked salt marsh were significantly lower than those in the natural salt

marsh for every season ( $p < 0.001$ ) (Figure S3). The soil pH and BD values in the embanked salt marsh were significantly higher than those in the natural salt marsh in every season ( $p < 0.001$ ) (Figure S3). However, no significant seasonal differences in the soil moisture, salinity, pH and BD were found in both the natural and embanked salt marshes ( $p \geq 0.05$ ) (Figure S3).

TABLE 1 Statistical significance of the effects of the embankment, seasons, and their interactions on (a) biomasses, N concentrations and storages of litter and roots, (b) soil organic N subpools, and (c) soil inorganic N subpools,  $R_A$  and  $R_N$  according to multi-way ANOVA.

(a)	LB ( $\text{kg}\cdot\text{m}^{-2}$ )	LNC ( $\text{g}\cdot\text{kg}^{-1}$ )	LNS ( $\text{g}\cdot\text{m}^{-2}$ )	RB ( $\text{kg}\cdot\text{m}^{-2}$ )	RNC ( $\text{g}\cdot\text{kg}^{-1}$ )	RNS ( $\text{g}\cdot\text{m}^{-2}$ )
Embankment	871.233***	83.822***	674.409***	93.928***	70.259***	35.725***
Season	352.875***	123.775***	208.441***	74.352***	21.704***	122.311***
Embankment $\times$ Season	85.788***	3.609*	50.940***	2.278	10.255***	4.602**
(b)	SON ( $\text{g}\cdot\text{kg}^{-1}$ )	LON ( $\text{g}\cdot\text{kg}^{-1}$ )	RON ( $\text{g}\cdot\text{kg}^{-1}$ )	DON ( $\text{g}\cdot\text{kg}^{-1}$ )	MBN ( $\text{mg}\cdot\text{kg}^{-1}$ )	
Embankment	109.285***	70.403***	158.889***	38.990***	6.982*	
Season	5.949***	10.374***	3.811*	45.073***	4.419**	
Embankment $\times$ Season	0.48	0.49	1.93	3.877*	4.244**	
(c)	$\text{NH}_4^+ - \text{N}$ ( $\text{mg}\cdot\text{kg}^{-1}$ )	$\text{NO}_3^- - \text{N}$ ( $\text{mg}\cdot\text{kg}^{-1}$ )	$R_A$ ( $\text{mg}\cdot\text{kg}^{-1}\cdot\text{d}^{-1}$ )	$R_N$ ( $\text{mg}\cdot\text{kg}^{-1}\cdot\text{d}^{-1}$ )		
Embankment	75.854***	3.37	22.937***	0.15		
Season	78.912***	29.813***	34.532***	4.989**		
Embankment $\times$ Season	3.017*	14.690***	19.34	20.30		

LB, litter biomass; LNC, litter nitrogen concentration; LNS, litter nitrogen storage; RB, root biomass; RNC, root nitrogen concentration; RNS, root nitrogen storage; SON, soil total organic nitrogen; LON, soil labile organic nitrogen; RON, soil recalcitrant organic nitrogen; DON, soil dissolved organic nitrogen; MBN, microbial biomass nitrogen;  $R_A$ , soil net ammonification rate;  $R_N$ , soil net nitrification rate. Asterisks indicate statistically significant at \*\*\* $p < 0.0001$ , \*\* $p < 0.001$ , \* $p < 0.05$ , and blanks indicate no significance at  $p \geq 0.05$ .

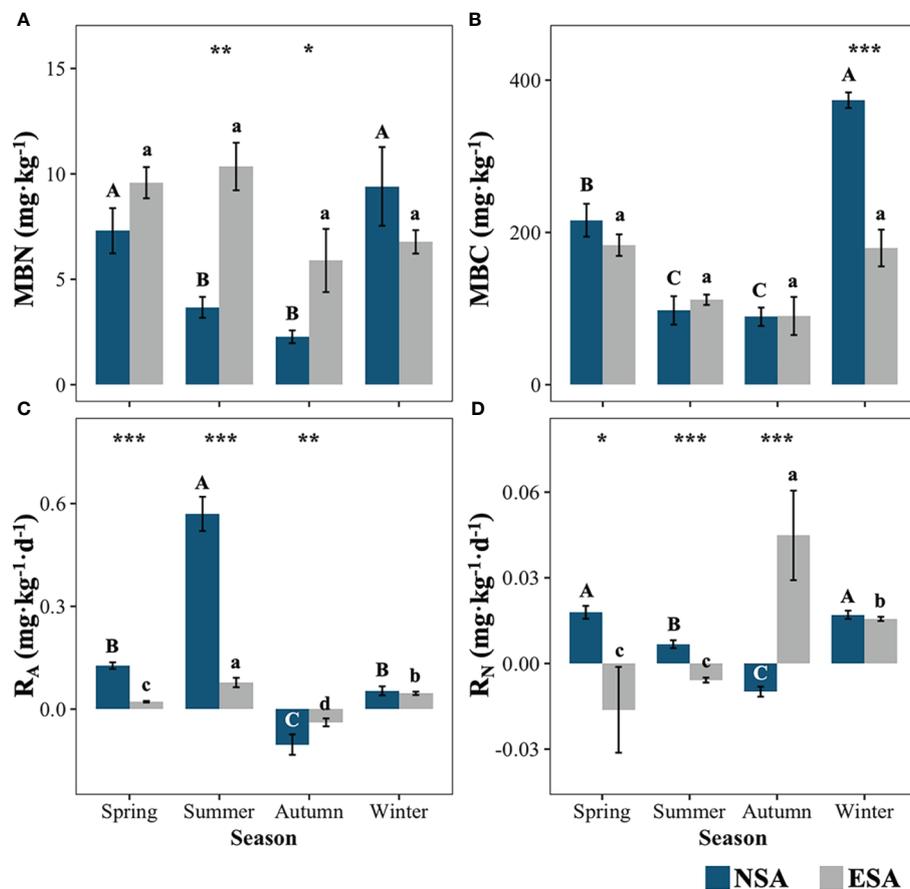


FIGURE 4

Values of the soil microbial biomass (A) nitrogen (MBN) and (B) carbon (MBC), and net soil (C) ammonification ( $R_A$ ) and (D) nitrification ( $R_N$ ) rate in natural (NSA) and embanked (ESA) *Spartina alterniflora* salt marshes in spring, summer, autumn, and winter. The averages and standard errors of four replicates are shown. Bars labelled with different uppercase and lowercase letters denote significant differences ( $p < 0.05$ ) between seasons in NSA and ESA, respectively. The differences between NSA and ESA were significant at \*\*\* $p < 0.001$ , \*\* $p < 0.01$  and \* $p < 0.05$ , and blanks indicate no significance at  $p \geq 0.05$ .

## Correlation analysis

The NMDS revealed that the soil N pool compositions in the embanked salt marsh were clustered and distinct from those in the natural salt marsh in every season (Stress < 0.001; Figure 5). Besides, the SON amounts highly correlated with the LNS values in natural salt marsh ( $p = 0.025$ ; Figure 6), whereas the relationship between the SON amounts and the LNS values in embanked salt marsh was insignificant ( $p = 0.1415$ ; Figure 6).

The results of SEM analyses are shown in Figure 7. It indicated a highly positive correlation between the N storage of each plant tissue and the biomass of the corresponding tissues in both the natural and embanked salt marshes. A remarkable positive correlation was found between the LON, RON, and LNS amounts in the natural salt marsh; a significantly positive relationship was observed between the DON and LNS amounts in the embanked salt marsh. The DON concentration was significantly and positively associated with the RNS value in the natural salt marsh; the LON concentration was dramatically positive correlation with the RNS value in the embanked salt

marsh. The  $\text{NH}_4^+ - \text{N}$  concentrations in both the natural and embanked salt marshes were significantly and negatively associated with the DON concentrations. The  $\text{NO}_3^- - \text{N}$  concentrations were significantly positively associated with those of  $\text{NH}_4^+ - \text{N}$ , but observably negative with the RNC values in both the natural and embanked salt marshes.

## Discussion

### The N storages in the plant subsystem

The storage of N in plants is a vital component of ecosystem N pools (Liu et al., 2017). A recent study has reported that coastal embankments can alter the N storage of plants by influencing their growth (Feng et al., 2022). In this study, the embankment was observed to significantly reduce the N storage and biomass of aboveground living tissue year-round (Figure 2). SEM analysis indicated that low soil salinity induced low aboveground living biomass in the embanked *S. alterniflora*

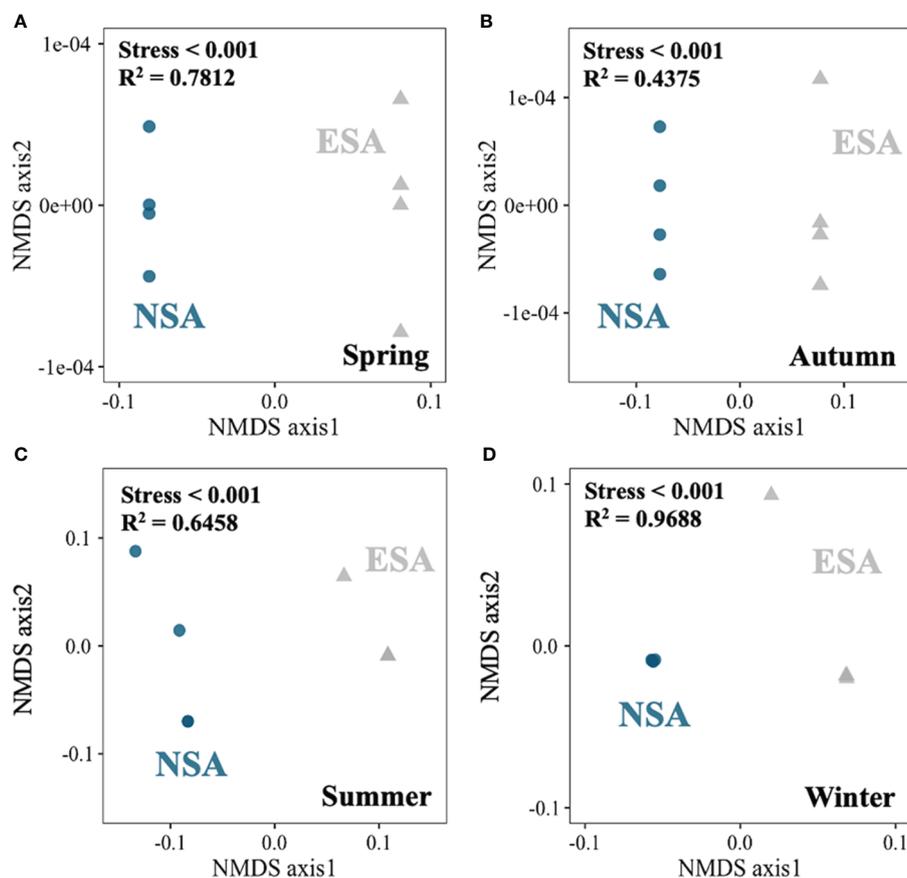


FIGURE 5  
Non-metric multidimensional scaling (NMDS) plot of dissimilarity of the edaphic N pools between the natural (NSA) and embanked (ESA) *Spartina alterniflora* salt marshes in (A) spring, (B) summer, (C) autumn, and (D) winter.

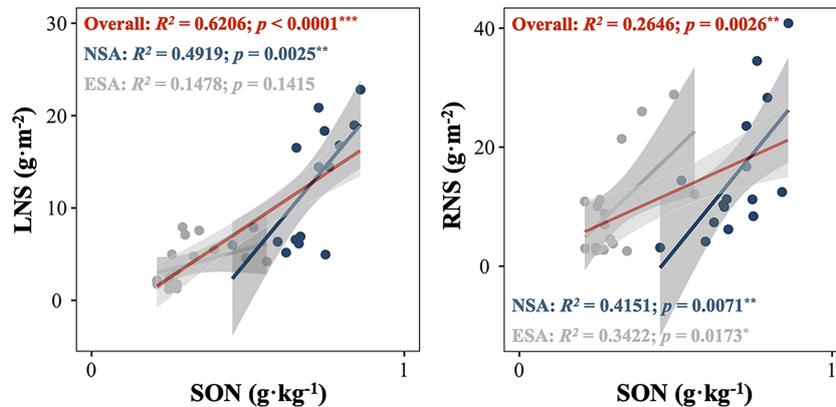


FIGURE 6

(A) Total soil organic nitrogen (SON) in relation to litter nitrogen storage (LNS) of *Spartina alterniflora*; (B) total soil organic nitrogen (SON) in relation to root nitrogen storage (RNS) of *S. alterniflora* in the natural (NSA) and embanked (ESA) salt marshes. Asterisks indicate statistically significant at \*\*\* $p < 0.0001$ , \*\* $p < 0.001$ , and blanks indicate no significance at  $p \geq 0.05$ .

salt marsh (Figure 7), which was supported by our recent study (Feng et al., 2022). This might have been attributed to the chlorophyll content and net *S. alterniflora* assimilation rate that are reduced under low-salinity conditions, which

decreases the generation of photosynthetic products and ultimately decreases the biomass (Ma et al., 2011). The decreased biomass of aboveground living tissues reduced their N storage (Figure 5). Furthermore, the decreased biomass and N

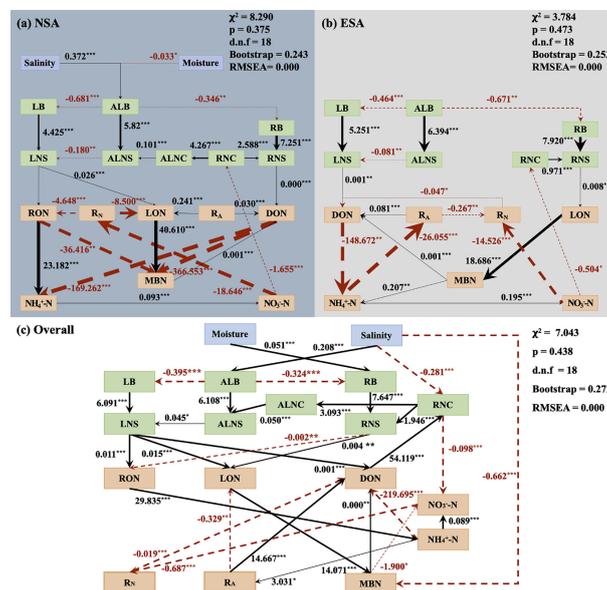


FIGURE 7

Nitrogen turnover among various nitrogen subpools in plant and soil subsystems in the (A) natural (NSA), and (B) embanked (ESA) salt marshes, as well as (C) their combine was examined by structural equation modelling (SEM). Solid and dashed arrows indicate positive and negative relationships, respectively. Numbers adjacent to arrows are the path coefficients (\*\* $p < 0.001$ , \* $p < 0.01$  and  $p < 0.05$ ). ALB, aboveground living biomass; ALNS, aboveground living nitrogen storage; ALNC, aboveground living nitrogen concentration; LB, litter biomass; LNS, litter nitrogen storage; LNC, litter nitrogen concentration; RB, root biomass; RNS, root nitrogen storage; RNC, root nitrogen concentration; SON, total soil organic nitrogen; DON, dissolved organic nitrogen; LON, labile organic nitrogen; RON, recalcitrant organic nitrogen; NH<sub>4</sub>-N, ammonia nitrogen; NO<sub>3</sub>-N, nitrite nitrogen; MBN, soil microbial biomass nitrogen; MBN, soil microbial biomass nitrogen; R<sub>n</sub>, soil net ammonification rate; R<sub>n</sub>, soil net nitrification rate.

storage of aboveground living tissues lowered the biomass and N storage of aboveground dead tissues (i.e., litter) in the embanked *S. alterniflora* salt marsh (Figure 7) (Jiang et al., 2009; Ma et al., 2011; Ge et al., 2015).

The embankment reduced the N storage of roots year-round, although it was insignificant in spring, summer, and autumn (Figure 2). SEM analysis suggested that low soil moisture could limit *S. alterniflora* root growth in the embanked salt marsh (Figure 7). This could be explained by *S. alterniflora* investing more nutrients for root growth when water resources were adequate, which enabled it to occupy more habitats (He et al., 2009). Further, this might reduce the tiller number and resource consumption by limiting the root growth when water was scarce (He et al., 2009). Thus, the decreased root biomass caused its N storage to be depressed (Figure 7). Besides, the temperature is generally considered as a vital factor which determines the plant growth (Elsey-Quirk et al., 2011). However, the root biomasses did not correlated with the temperature any more in the embanked salt marsh, which indicated that the embankment altered the seasonal variation of the root growth (Figure S4). This may be because the embankment altered the physiological process of *S. alterniflora* by changing the soil physicochemical properties, which affected its response to the temperature (Shi and Bao, 2007). In summary, since soil salinity and moisture are two critical drivers that influence plant growth in salt marshes, the coastal embankment reduced the N storage of *S. alterniflora* by restricting plant growth through decreased soil salinity and moisture (Figure 7).

## The organic N subpool in the soil subsystem

The embankment drastically shrunk the size and modified compositions of the soil N pool in *S. alterniflora* salt marsh in every season (Figures 3, 5). The organic N subpool is an essential element of ecosystem N pools (Feyissa et al., 2020), while it regulates net plant primary production in most ecosystems and typically sensitive to changes in plant N storage (Jones et al., 2004; Chen et al., 2017; Feng et al., 2017). This is because soil organic matter was derived from the biodegradation of plant debris and dead roots (Figure 7; Zhou et al., 2015; Li et al., 2018). Thus, the embankment remarkably decreased the N storage of *S. alterniflora* litter and roots, which further reduced the size of the organic N subpools (e.g., SON, LON, RON, and DON) for every season (Figures 2, 3, 6).

The embankment also changed the N turnover from the plant subsystem to the soil subsystem in the *S. alterniflora* salt marsh, for example, the plant litter N storage (i.e., LNS) did not make the contribution to the size of the soil organic N subpool (i.e., SON) due to the embankment (Figures 6, 7). RON is generally composed of organics that are recalcitrant to decomposition (Lin et al., 2016; Xi et al., 2020; Xi et al., 2021).

According to SEM analysis, the RON in the natural salt marsh was primarily derived from organic litter inputs (Figure 7). This was because lignin and lignocellulosic are rich in *S. alterniflora* litter, where the roots may not contain abundant refractory materials (Zeng et al., 2020; Feng et al., 2022). However, the effects of the litter N storages on the RON amount were negligible in the embanked salt marsh, which was possibly due to the litter N storage observably decreased due to the embankment (Figures 3, 7).

LON comprises the active component of the soil organic N subpools (Lin et al., 2016; Xi et al., 2020; Xi et al., 2021). The embankment also changed the source of LON, and the organic N inputs was from the litter in the natural salt marsh to the roots in the embanked salt marsh (Figure 7). This was probably also because the dramatically decreased litter and root N storage due to the embankment (Figure 2). However, the embankment did not alter the seasonal variation of LON (Figure 3). Generally, LON was more responsive to changes in plant N inputs compared to RON (Feyissa et al., 2020). On the coast of Jiangsu, the ALB of *S. alterniflora* attained a maximum in summer and autumn (Zhao et al., 2005; Zhang et al., 2010). Thus, the limited death of the aboveground *S. alterniflora* tissues led to a low LB in summer and autumn (Zhao et al., 2005; Zhang et al., 2010). Furthermore, the roots of *S. alterniflora* are nutrients storage tissues (Lawrence et al., 2013; Zhao et al., 2016). During the growing season, nutrients stored by roots were transported to support aboveground plant growth, thus the LB was low (Lytle and Hull, 1980; Lana et al., 1991; Chen et al., 2014). Therefore, lower LB and RB led to low LNS, RNS, and LON during summer and autumn for both natural and embanked *S. alterniflora* salt marshes (Figures 2, 3). In spring and winter, the aboveground living organs of *S. alterniflora* died and were transformed to litter; thus, high values of LB were observed (Figures 2, 3, 7) (Chen and Xu, 2006; Zhou et al., 2015). Additionally, *S. alterniflora* rapidly occupied habitats through the vegetative reproduction of its roots at the beginning of the growth season, and as a result the highest level of RB was observed in spring (Figure 2). Therefore, the elevated LB and RB resulted in the high LNS, RNS, and LON in spring and winter for both the natural and embanked *S. alterniflora* salt marshes (Figures 2, 3).

DON is the most active portion of the soil organic N subpool (Rentsch et al., 2007; Cott et al., 2020), which includes low-molecular weight compounds (e.g., amino acids, polypeptides, and purines) and high-molecular weight compounds (e.g., proteins and chlorophyll) (Quan et al., 2022). In this study, we found that the organic N inputs from roots was the primary source of DON in the natural salt marsh (Figure 7). This was possibly because the living roots could exude various low-molecular weight compounds (e.g., organic acids and sugar), meanwhile the decomposition of the death roots also promoted the accumulation of DON (Chen and Xu, 2006; Zhou et al., 2015). However, the DON in the embanked salt marsh mainly

came from the organic N inputs from litter, which was explained by the passive leaching of soluble organic matter from litter in the soil (Figure 7; Chen and Xu, 2006; Zhou et al., 2015). Further, according to the SEM analysis, MBN was an additional important source of DON in the natural and embanked *S. alterniflora* salt marsh (Figure 7). This might be due to DON having the capacity to be released into the soil after microbial death (Isobe et al., 2018; Evangelou et al., 2021; Heinzle et al., 2021).

## The inorganic N subpool in the soil subsystem

The embankment not only changed the process of the organic N inputs from the plant subsystem to the soil subsystem, but also altered the N turnover from the organic N subpools into the inorganic N subpools in the soil subsystem (Figure 7). Generally, the generation of inorganic N in soil is regulated by its organic N content (Cartaxana et al., 1999; Cott et al., 2020). SEM analysis indicated that the major contributor of the soil  $\text{NH}_4^+ - \text{N}$  was RON in the natural salt marsh (Figure 7). Prior studies reported that bacteria and fungi, which can degrade high-molecular weight substances (e.g., RON), were rich in the *S. alterniflora* sediment (Yang et al., 2021; Feng et al., 2022). However, there was lack of contribution of RON to the soil  $\text{NH}_4^+ - \text{N}$  in the embanked salt marsh, because there was inappreciable organic N input from the litter or roots to the soil RON (Figure 7). Additionally, according to the SEM analysis, an increased soil  $\text{NH}_4^+ - \text{N}$  content can lead to decreased DON in the natural and embanked salt marshes (Figure 7). Since DON is rich in a variety of amino acids it can be mineralized to release  $\text{NH}_4^+ - \text{N}$  through the microbial generation of extracellular enzymes (Berman and Bronk, 2003; Schimel and Bennett, 2004; Geisseler et al., 2009; Xing et al., 2010). Therefore, we speculated that DON is also a non-negligible source of  $\text{NH}_4^+ - \text{N}$  in the soil of *S. alterniflora* salt marshes, where lower DON may lead to reduced  $\text{NH}_4^+ - \text{N}$  in the soil following the establishment of the embankment. In summary, microorganisms may produce  $\text{NH}_4^+ - \text{N}$  by decomposing the organic N; thus, the embankment significantly diminished the quantities of  $\text{NH}_4^+ - \text{N}$  by shrinking the size of the organic N (e.g., RON, and DON) year-round (Figures 3, 7; Feng et al., 2022).

$\text{NO}_3^- - \text{N}$  is another primary inorganic form of N that is intimately related to  $\text{NH}_4^+ - \text{N}$  due to soil nitrification (Figure 7) (Ueda et al., 2013; Augustine et al., 2014; Nguyen et al., 2017). Thus, the concentrations of  $\text{NO}_3^- - \text{N}$  decreased under lower  $\text{NH}_4^+ - \text{N}$  concentrations in summer, autumn, and winter after the establishment of the embankment (Figure 7). Nevertheless, the  $\text{NO}_3^- - \text{N}$  concentration increased significantly in spring following embankment development (Figure 3). Thus, we speculated that, (1) nitrification might continue in spring, even

when the soil  $\text{NH}_4^+ - \text{N}$  concentration was low (Augustine et al., 2014; Schütt et al., 2014; Heinzle et al., 2021); (2) the rapid decrease in  $\text{NO}_3^- - \text{N}$  utilization by plants at the onset of plant growth occurred in spring due to the dramatically decreased plant biomass following the establishment of the embankment (Augustine et al., 2014; Che et al., 2018; Heinzle et al., 2021).

## Microbial N mineralization and immobilization

Organic soil N is converted to inorganic N via N mineralization, which is influenced by multiple factors (Zhou et al., 2015; Nguyen et al., 2017). In this study,  $R_A$  in the embanked salt marsh decreased significantly in spring and summer but rapidly increased in autumn (Figure 4). Previous studies have reported that the soil N mineralization rate was determined by microbial activities, which are always highly associated with the temperatures (Augustine et al., 2014; Lozano-García et al., 2016; Heinzle et al., 2021). For example, higher temperatures can stimulate microbial activities, which directly expedite the soil N turnover rate (Lozano-García et al., 2016). In the study, we found  $R_A$  was positive correlation with temperatures in the natural salt marsh, whereas the association between  $R_A$  and temperatures was not observed in the embanked salt marsh (Figure S4). This result indicated that the embankment probably dramatically modified the microbial responses to the temperature changes, which ultimately altered the seasonal variation of  $R_A$  (Figure 4). Simultaneously, the maximum and minimum  $R_A$  values were observed in summer and autumn, respectively, in both the natural and embanked salt marshes (Figure 4). Organic soil N, particularly DON, serves as a vital mineralization substrate that drives the rate of soil N mineralization (Figure 7; Montano et al., 2007; Näsholm et al., 2009). In fact, previous studies have reported that soluble organic matter can provide energy for heterotrophic microorganisms, which is favored for higher levels of N mineralization (Montano et al., 2007; Näsholm et al., 2009). This was supported by the SEM analysis of this study (Figure 7). The highest and lowest DON amounts were observed in summer and autumn, respectively; thus, the seasonal variations in  $R_A$  may be contributed to by those of the DON content (Figures 3, 4). Besides, enhanced microbial activities and accelerated soil N turnover rates under increased temperatures stimulated  $R_A$  in summer and autumn either (Figures 3, 7; Augustine et al., 2014; Lozano-García et al., 2016; Heinzle et al., 2021).

Furthermore, the  $R_N$  decreased significantly in spring and summer, while it increased to a considerable degree in autumn following the establishment of the embankment (Figure 4). These changes were consistent with the variations in  $R_A$  following embankment development, as organic matter initially mineralized to  $\text{NH}_4^+ - \text{N}$ . Subsequently,  $\text{NO}_3^- - \text{N}$  was derived from the nitrification of  $\text{NH}_4^+ - \text{N}$  (Figure 4; Khalsa et al., 2020).

Microbial immobilization is also a crucial process in the soil N cycle, as organic and inorganic N can be assimilated by microbes and rapidly converted to MBN (Fahey et al., 2011; Nguyen et al., 2017). In this study, high LON concentrations promoted the accumulation of MBN in the natural and embanked salt marshes according to the SEM analysis, which suggested that soil LON was a vital N source for microorganisms (Figure 7). Nevertheless, the embankment observably decreased the soil LON, but it dramatically elevated the MBN amount in summer and autumn (Figures 3, 4). Besides, earlier studies reported that MBN was closely and positively correlated with MBC, SOC, and SON in general. Whereas in this study, MBC concentrations did not increase significantly, and concentrations of SOC and SON prominently decreased in summer or autumn (Figures 3, 4; Manirakiza et al., 2019). Therefore, the increased MBN content was not caused by lower concentrations of LON, MBC, SOC, or SON. SEM analysis revealed that the decreased soil salinity following embankment establishment raised the concentration of MBN (Figure 7). Salinity is a vital factor that drives the growth of microbes in coastal wetlands due to its being the determinant of the osmotic potential of the soil (Gao et al., 2012). Consequently, the decreased soil salinity induced an increased solution osmotic potential, which ultimately enhanced the uptake of ions (e.g.,  $\text{NO}_3^- - \text{N}$ ) by microbes and stimulated the production of MBN in the embanked *S. alterniflora* salt marsh (Figure 7) (Mavi and Marschner, 2013).

## Plants N absorption

The soil N pool is not only the N sink but also the N source for plants in salt marshes (Geisseler et al., 2009). Soil inorganic N is the primarily source of N for plants (Jones et al., 2004; Jones et al., 2005). Based on SEM analysis, increased RNC led to decreased soil  $\text{NO}_3^- - \text{N}$  but had little impact on soil  $\text{NH}_4^+ - \text{N}$  (Figure 7). This indicated that *S. alterniflora* possessed a greater capacity to take up  $\text{NO}_3^- - \text{N}$  rather than  $\text{NH}_4^+ - \text{N}$  from soil (Jones et al., 2005). This was possibly due to  $\text{NO}_3^- - \text{N}$  not being easily adsorbed by soil particles with negative charges, and its easy leaching into the soil for take up by plants (Jones et al., 2005). Besides, according to the SEM analysis, increased soil DON stimulated RNC, which indicated that DON is another essential available source of N supplies for plant uptake (Figure 7; Kerley and Read, 1995; Alexandre et al., 2015; Cott et al., 2020). Earlier studies revealed that plants can acquire a wide variety of low molecular weight N compounds from DON as the N source, *via* roots when they grow rapidly (e.g., amino acids, amino sugars, and peptides) (Kerley and Read, 1995; Alexandre et al., 2015; Cott et al., 2020). Soil N (e.g.,  $\text{NO}_3^- - \text{N}$  and DON) can be absorbed by roots, which promoted the growth and N storage of roots (i.e., RB and RNS). Moreover, the N absorbed by roots can be transferred from root tissues to aboveground living tissues,

which promote their N storage (i.e., ALNS) in the natural salt marsh (Figure 7). However, the embankment seems stop the N transfer from root tissues to aboveground living tissues (Figure 7). Therefore, the embankment also converted N absorption of plants (Figure 7).

## Conclusion

The coastal embankment dramatically reduced the plant N storage and the soil N pool in the *S. alterniflora* salt marsh year-round, and modified the N transfer processes in the plant subsystem and soil subsystem. Firstly, the litter and root biomass of *S. alterniflora* were significantly decreased due to the lower soil salinity and moisture in the embanked salt marsh, compared to those in the natural salt marsh for every season. Further, the decreased litter and root biomass of *S. alterniflora* translated to the remarkable reduction of N storage in the embanked salt marsh year-round. Secondly, due to the decreased N inputs from plants, the soil organic N subpool (e.g., SON, RON, LON, DON) was observably reduced during every season to varying degrees. Thirdly, the embankment also significantly diminished most of the soil inorganic N subpool (i.e.,  $\text{NH}_4^+ - \text{N}$  and  $\text{NO}_3^- - \text{N}$ ) which was regulated by the diminution of the organic N content (e.g., RON and DON). Fourthly, although the sizes of the soil organic and inorganic N subpools were reduced, the soil MBN concentrations increased in spring, summer, and winter at different levels due to the embankment. We suggest that the decreased soil salinity following the development of the embankment induced a higher osmotic potential, which ultimately increased the uptake of ions (e.g.,  $\text{NO}_3^- - \text{N}$ ) by microbes, while stimulating the production of MBN. Ultimately, the soil  $\text{NO}_3^- - \text{N}$  and DON were two vital N sources for *S. alterniflora*, and plants absorbed N from the soil and promote their biomass, N concentrations, and storage (e.g., RB, RNC, RNS, ALB, ALNS). Our study is conducive toward further understanding the mechanisms behind the effects of coastal embankments on the seasonal variations in plant-soil N pools.

## Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding authors.

## Author contributions

GQ: writing – original draft. HF: conceptualization, software, formal analysis, data curation, and writing – original draft. HZ: methodology and investigation. LX:

conceptualization, methodology, software, formal analysis, data curation, writing – original draft, writing – review and editing, and visualization. WY: conceptualization and methodology. YZ: methodology, resources, and investigation. NJ: writing – review and editing. SA: conceptualization, resources, writing – review and editing, project administration, and funding acquisition. All authors contributed to the article and approved the submitted version.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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## Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.959144/full#supplementary-material>.

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