ECOLOGICAL STOICHIOMETRIC CHARACTERISTICS OF THE MANGROVE ECOSYSTEM IN BEIBU GULF, CHINA

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Abstract. Despite extensive studies on how environmental factors influence plant and soil nutrient distribution and stoichiometry, how the intertidal zone affects plant and soil distribution, and stoichiometry remains unclear. Therefore, this study analyzed the leaf and soil organic carbon (C), nitrogen (N), and phosphorus (P) concentrations and stoichiometry in mangrove forest wetlands in South China. The results demonstrated that leaf and soil phosphorus concentrations were significantly different in different plants and intertidal zones. The average leaf N:P ratio was 12.85 and was mainly nitrogen-limited. Soil organic carbon at 0–10 cm was higher in the mid- and low intertidal zones, while the opposite was true for the high intertidal zone. The nitrogen concentration at 0–10 cm was less than that at <30–40 cm in both the high and mid-intertidal zones, while the opposite was true for the low intertidal zone. The phosphorus concentration varied similarly to that of carbon. The C:N ratios at both 0–10 cm and 30–40 cm were the highest in the high intertidal zone and decreased with decreasing elevation. Contrastingly, the C:P and N:P ratios did not differ much among the three intertidal zones and between the 0–10-cm and 30–40-cm profiles. The soil C:N ratios significantly correlated with the leaf carbon, phosphorus, and C:P ratio. Overall, the results demonstrated that the soil stoichiometry responded differently to different plant communities and intertidal zones. These differences might be attributed to variations in the environmental conditions of plant communities.
Keywords: *intertidal, C, N, P, soil nutrients, plant nutrients, South China*

Introduction

Carbon (C), nitrogen (N), and phosphorus (P) are the primary elements essential for the structure and function of all organisms and ecosystems (Elser et al., 2003). Carbon can be measured with other important elements in organic tissue and comprises approximately 50% of dry matter (Hessen et al., 2004). Nitrogen is important in all enzymatic activity, and phosphorus is a vital element for genetic material and RNA and ATP energy storage (Chen et al., 2013). These three elements are strictly coupled in organic tissue. Ecology stoichiometry is the study of the mass balance of multiple chemical elements in ecological systems (Andersen et al., 2004; Elser et al., 2007). It is useful for understanding the links between trophic interactions and nutrient cycling (Qu et al., 2014). Furthermore, C:N:P ratios are excellent for explaining how the elemental composition of organism growth combines with the inorganic environment (Lü et al., 2013), such as specific composition and plant biodiversity (Güsewell et al., 2010) and the tolerance of organisms when adapting to environmental stress (Woods et al., 2003).

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Mangrove plants grow in tropical and subtropical regions, are typically subject to periodic inundation by tidal waters, and are mainly found on deeply silted bays or estuarine saline soils (Pires et al., 2012). Mangrove forests are important vegetation in the coastal intertidal zone and have various ecological functions, such as preventing sea level rise, promoting siltation and land formation, purifying the environment, and protecting marine biodiversity. Additionally, mangrove forests also contribute much economic value to human beings as industrial raw materials such as wood, food, medicine, and tannin (Zheng et al., 2023). In 2000, the global mangrove area was ~137,760 km^2, accounting for 0.7% of tropical forests globally. The global mangrove area is distributed in Asia (42%), Africa (20%), North America (15%), Oceania (12%), and South America (11%) (Giri et al., 2011) and comprises a total of 83 species from 24 families and 30 genera. In China, the mangrove forest covers an area of ~34472.14 hm^2 and has 12 families, 16 genera, and 24 species (Dan et al., 2016). The Chinese mangrove area is distributed in the coastal areas of the Zhejiang, Fujian, Guangdong, and Guangxi provinces and the coastal beaches of Hainan Island and Hong Kong, Macao, and Taiwan. However, the growth of the Chinese population, social and economic improvement, unusually rapid urban expansion, especially the rapid development of coastal cities, various anthropogenic activities, exotic species invasion, and other phenomena have shrunk the mangrove area and degraded the environment. Therefore, analyzing the relationship between mangrove plants and the environment and strengthening mangrove forests' ecological and environmental management is particularly important for the ecological environment and climate change.

Mangroves are found in tidal wetlands that are periodically inundated by tides. Tidal wetlands can be categorized into high-, mid-, and low-tide zones. The mangrove vegetation distribution in different intertidal zones is affected by tides, salinity, pH, and other factors. Plant carbon, nitrogen, and phosphorus concentrations are important elemental indicators of ecosystem processes, and changes in their concentrations and ratios can reflect elemental exchange processes and the ecological functions of plant communities. Currently, mangrove research focuses on population dynamics, benthic organisms, heavy metals, carbon sinks, wetland remote sensing monitoring, and conservation analysis (Yue et al., 2017; Zhou et al., 2020). However, there are fewer studies on the ecological chemometric characteristics of mangrove ecosystems in Guangxi. The elemental carbon, nitrogen, and phosphorus concentrations and ratios in different intertidal zones differ due to hydrological factors. The research subjects in this study were *Bruguiera gymnorrhiza*, *Kandelia obovata*, *Aegiceras corniculatum*, and *Auicennia maeina*. The characteristics of nutrient concentration and stoichiometry of the leaves from the above four mangrove plants and soils in different intertidal zones were examined, and the relationship between plant growth mechanisms and environmental factors was investigated.

Materials and methods

Study area

Beilun Estuary National Nature Reserve (21°31’00”–21°37’30”N, 108°00’30”–108°16’30”E) is located at the southwestern coastal strip of Fangchenggang City, Guangxi, China. The reserve spans Pearl Bay, the three islands of Jiangping, and the mouth of the Beilun River from east to west, borders Beibu Gulf in the southeast, and adjoins Vietnam in the southwest. The shoreline is 105-km long, the mudflat area is

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53 km^2, and the existing mangrove area is ~1,274 hm^2. The reserve is in the southern subtropical oceanic monsoon climate zone and has a warm and hot climate, with an average annual temperature of 22.3 °C, extreme maximum temperature of 37.8 °C, extreme minimum temperature of 2.8 °C, and average annual precipitation of 2,220.5 mm (Liu et al., 2012). Precipitation at the reserve is mainly concentrated in June to August. The average annual evaporation is 1,400 mm. The dominant mangrove plants are *K. obovata*, *B. gymnorrhiza*, *A. maeina*, and *Aegiceras corniculatum*.

Field survey

In October 2018, four transects were established in three intertidal zones (high, middle, and low). Each sample plot was 400 m^2 (20 m × 20 m) and was divided into four 10 m × 10 m sample units. Five well-developed plants from each studied species were selected in each plot. Twenty to forty mature, pest-free leaves from the canopy periphery were selected and brought to the laboratory in self-sealing bags. The leaves were dried at 70 °C for 48 h to measure the leaf carbon, nitrogen, and phosphorus concentrations. At each location, soil samples were taken using a stainless-steel soil corer with a diameter of 9.6 cm. Soil was collected from 0–10 cm and 30–40 cm for nutrient concentration measurement and ecological stoichiometric characterization. The soil samples were collected using five-point sampling using the four corners and center point of each sample plot as sampling points. The collected soil was brought to the laboratory, dried naturally, and then ground and bagged for soil nutrient concentration measurement (*Figure 1*, *Table 1*).

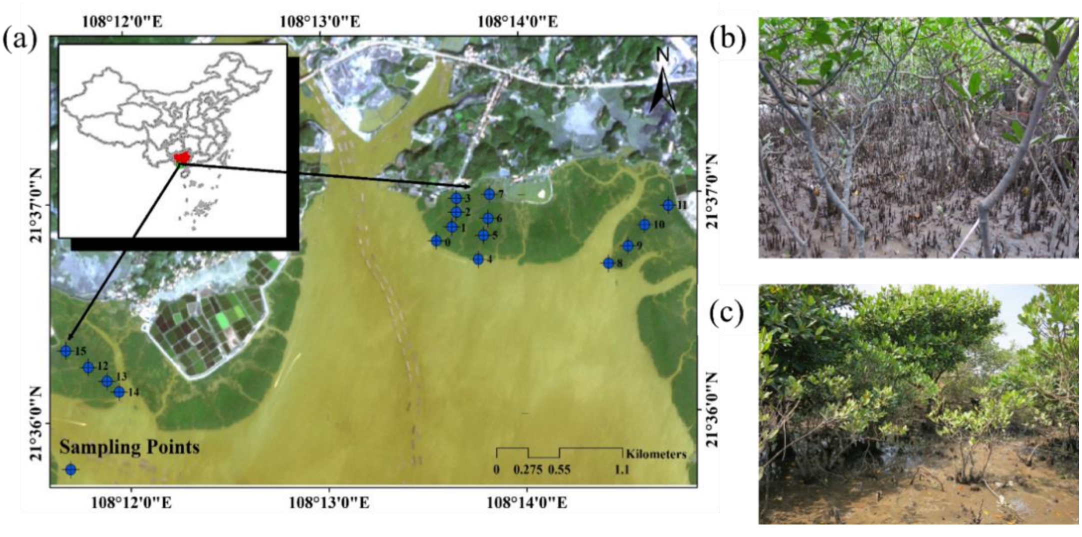

Figure 1. *(a)Map of soil sample collection locations;(b) and (c) sampling environment in the study*

Laboratory analysis

The leaf total carbon (TC) and total nitrogen (TN) concentrations were measured using a vario MAX CN Element Analyzer (Elementar, Hanau, Germany). The leaf total phosphorus (TP) concentration was measured by colorimetric analysis using a TU-1901 spectrophotometer (Thermo Fisher Scientific, Delft, The Netherlands) after pre-treatment with H_2SO_4–H_2O_2 digestion (Zhang et al., 2015).

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Table 1. *Coordinates of sampling sites*

Sampling site	Longitude	Latitude	Intretidal
0	108.226044	21.613317	Low intertidal
1	108.2274	21.614351	Low intertidal
2	108.227793	21.615475	Middle intertidal
3	108.227816	21.61652	High intertidal
4	108.229551	21.611845	Low intertidal
5	108.230035	21.613669	Low intertidal
6	108.230447	21.61495	Middle intertidal
7	108.23061	21.616781	High intertidal
8	108.240517	21.61133	Low intertidal
9	108.242201	21.612635	Low intertidal
10	108.243625	21.614211	Middle intertidal
11	108.24566	21.615661	High intertidal
12	108.19651	21.60421	Middle intertidal
13	108.198069	21.60313	Low intertidal
14	108.199072	21.602287	Low intertidal
15	108.194649	21.605512	High intertidal

Soil organic carbon (SOC) concentrations were measured using the $K_2Cr_2O_7$–H_2SO_4 oxidation method (Zhang et al., 2009). Soil TN concentrations were measured using a Carlo Erba CNS Analyzer (Carlo Erba, Milan, Italy). Soil TP concentrations were measured via perchloric acid digestion followed by ammonium molybdate colorimetry (Wang et al., 2006). The units (mg g^{-1}) of carbon, nitrogen, and phosphorus concentrations were transformed to mol kg^{-1} to calculate the C:N, C:P, and N:P ratios of each sample as the molar ratio (atomic ratio).

Data analysis and statistics

The significance of the leaf carbon, nitrogen, and phosphorus concentrations and C:N, C:P, and N:P ratios in the four mangrove species and three intertidal zones were tested using two-way analysis of variance. Relationships between nutritional elements and ratios were determined by correlation analysis. Multiple comparisons of the means were performed using Tukey's test at the 0.05 significance level. All statistical analyses were performed using SPSS 20 (SPSS Inc., Chicago, IL, USA).

Results

Leaf carbon, nitrogen, and phosphorus stoichiometry

Leaf carbon concentrations (396.82–411.24 mg g^{-1}) were the highest in *Aegiceras corniculatum*, while leaf nitrogen and phosphorus concentrations (16.11–16.36 mg g^{-1} and 1.63–1.79 mg g^{-1}, respectively) were the highest in *A. maeina* in different intertidal zones. Leaf carbon concentrations were not significantly different among the three intertidal zones and among the four mangrove species ($P > 0.05$). Leaf nitrogen concentrations were significantly different among the four mangrove species: concentrations in *B. gymnorrhiza* and *A. maeina* were as follows: high intertidal zone > mid-intertidal zone > low intertidal zone ($P < 0.05$), while the opposite was true for *Aegiceras corniculatum*, which was not significantly different among the three intertidal

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zones ($P > 0.05$). Leaf phosphorus concentrations were significantly different among the three intertidal zones and four mangrove species ($P < 0.05$) (low intertidal zone > high intertidal zone > mid-intertidal zone). The leaf phosphorus concentrations in *B. gymnorrhiza* and *Aegiceras corniculatum* were increased with elevation, while the opposite was true for *A. maeina* (*Table 2*).

Table 2. *Carbon, nitrogen, and phosphorus contents and stoichiometric ratios of mangrove leaves on different gradients in the Beilun estuary intertidal zones*

		TC (mg g-1)	**TN (mg g-1)**	**TP (mg g-1)**	**C:N**	**C:P**	**N:P**
High intertidal	*Bruguiera gymnorrhiza*	384.18±7.58ab	12.29±2.74b	0.69±0.07c	32.76±8.65a	564.08±63.4a	17.81±3.36a
	Auicennia maeina	360.54±17.65c	16.36±2.03a	1.79±0.30a	22.33±3.17c	207.37±45.33c	9.3±1.61c
	Kandelia obovata	402.50±8.51a	12.19±1.61b	0.95±0.04b	33.72±6.24a	425.06±6.24b	12.91±1.94b
	Aegiceras corniculatum	407.29±3.47a	11.44±1.24c	0.94±0.14b	35.98±4.25a	441.85±68.1b	12.25±0.82b
Middle intertidal	*Auicennia maeina*	360.35±3.92c	16.36±0.91a	1.64±0.05a	22.08±1.14c	219.57±6.63c	9.96±0.28c
	Kandelia obovata	400.32±10.15a	14.65±1.29ab	0.90±0.11b	27.47±2.57b	447.17±50.43b	16.5±3.56a
	Bruguiera gymnorrhiza	368.79±12.82c	10.95±0.73d	0.70±0.04c	33.81±2.44a	529.18±31.34a	15.71±1.33a
	Aegiceras corniculatum	411.24±7.08a	11.87±1.01c	0.96±0.10b	34.85±3.13a	433.38±47.22b	12.42±0.36b
Low intertidal	*Auicennia maeina*	347.68±10.14d	16.11±0.96a	1.63±0.17a	21.65±1.67c	215.42±28.65c	9.93±0.8c
	Kandelia obovata	384.46±11.16b	12.93±1.03b	0.97±0.06b	29.88±2.25b	399.35±32.36bc	13.43±1.46b
	Aegiceras corniculatum	396.82±9.58ab	12.00±1.02b	1.00±0.11b	33.33±3.5a	404.47±55.34bc	12.13±0.87b

Note: The values in the table are average ± standard error; different letters indicate significant differences between the leaves of each plant

The C:N ratios were increased with elevation (21.65–35.98) and were significantly different in the four species in the three intertidal zones ($P < 0.05$). The C:P ratios varied considerably among the four species in the three intertidal zones, where the *B. gymnorrhiza* C:P ratio (564.08) was twice as high as that of *A. maeina* (207.37) in the highest intertidal zone ($P < 0.05$). Similar to the C:P ratio, the N:P ratio first increased and then decreased with increasing elevation. The N:P ratio in *A. maeina* was lower than that of the studied species in the three intertidal zones (*Table 2*). A two-way ANOVA showed that intertidal and vegetation types had different effects on leaf C, N, P concentrations and ratios (*Table 3*).

Soil carbon, nitrogen, and phosphorus stoichiometry

Soil organic carbon concentrations (7.17–42.63 mg g^{-1}) were the highest at 30–40 cm in the high intertidal zone and lowest at 30–40 cm in the low intertidal zone. Soil nitrogen concentrations (0.12–2.18 mg g^{-1}) were also the highest at 30–40 cm in the high intertidal zones, while lowest at 0-10 cm in middle intertidal zone. Soil phosphorus concentrations (0.1–0.38 mg g^{-1}) were also the highest at 30-40 cm in the high intertidal zones and were

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lowest at 30–40 cm in the middle intertidal zone. However, the soil organic carbon, nitrogen, and phosphorus concentrations were not significantly different in the three intertidal zones ($P > 0.05$) (*Table 4*). The soil C:N ratios (15.22–58.68) increased with elevation. The soil N:P ratios (1.21–6.33) were the highest at 30–40 cm in the middle intertidal zones, while lowest at 0-10 cm in the high intertidal zones. The soil C:P ratios (41.72–121) were higher at 30–40 cm in the middle intertidal zones, and lowest at 0-10 cm in the low intertidal zones. However, the soil C:N, C:P, and N:P ratios were not significantly different among the three intertidal zones ($P > 0.05$) (*Table 4*). A two-way ANOVA showed that intertidal and soil depth had no significantly effect on soil C, N, P concentrations and ratios (*Table 5*).

Table 3. *Summary of two-way ANOVAs on leaf concentrations of TC, TN, and TP, and ratios of C:N, C:P, and N:P in different intertidal and vegetation types (F-values)*

	Intertidal		**Vegetation types**		**Intertidal*Vegetation types**	
	F	**P**	**F**	**P**	**F**	**P**
TC (mg g^{-1})	6.967	0.002	69.777	0.000	1.100	0.375
TN (mg g^{-1})	0.601	0.552	32.932	0.000	1.639	0.155
TP (mg g^{-1})	0.510	0.603	144.648	0.000	0.947	0.470
C:N	0.792	0.458	26.602	0.000	0.814	0.564
C:P	1.433	0.248	110.369	0.000	0.697	0.653
N:P	1.516	0.229	29.549	0.000	2.655	0.025

Table 4. *Soil carbon, nitrogen, and phosphorus contents and stoichiometric ratios in different intertidal zones at different depths in the Beilun estuary*

Intertidal	**Soil depth (cm)**	**SOC (mg g^{-1})**	**TN (mg g^{-1})**	**TP (mg g^{-1})**	**C:N**	**C:P**	**N:P**
Low intertidal	0-10	15.24±1.63	0.73±0.09	0.21±0.02	21.46±1.7	73.27±7.66	3.46±0.32
	30-40	13.84±1.82	0.64±0.1	0.19±0.01	21.94±0.82	74.01±8.56	3.38±0.36
Middle intertidal	0-10	14.73±1.21	0.59±0.06	0.18±0.01	26.23±1.91	84.67±7.7	3.3±0.33
	30-40	14.59±0.96	0.62±0.08	0.17±0.01	24.85±1.88	87.76±4.61	3.65±0.3
High intertidal	0-10	17.07±3.57	0.77±0.22	0.21±0.03	27.42±4.2	79.04±6.95	3.28±0.55
	30-40	18.92±4.35	0.86±0.25	0.22±0.03	27.74±4.66	79.84±7.14	3.36±0.56

Note: The values in the table are average ± standard error; there were not significantly different among the three intertidal zones

Correlations among carbon, nitrogen, and phosphorus concentrations and stoichiometry

The SOC concentration was significantly positively correlated with leaf N concentration, C:N ratio, and negatively correlated with the leaf P concentration, C:P and N:P ratio ($P < 0.05$). Soil N concentration was negatively with leaf N concentration ($P < 0.05$). Soil C:P was significantly positively correlated with the leaf N concentration and negatively with leaf C:N ratio ($P < 0.05$). Soil N:P ratio was positively with leaf N:P ratio. The correlation between the other values was not significant ($P > 0.05$) (*Table 6*).

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Table 5. *Summary of two-way ANOVAs on leaf concentrations of SOC, TN, and TP, and ratios of C:N, C:P, and N:P in different intertidal and soil depth (F-values)*

	Intertidal		**Soil depth**		**Intertidal*Soil depth**	
	F	**P**	**F**	**P**	**F**	**P**
SOC (mg g^{-1})	1.153	0.325	0.002	0.962	0.202	0.818
TN (mg g^{-1})	0.942	0.398	0.009	0.923	0.187	0.830
TP (mg g^{-1})	2.267	0.116	0.099	0.755	0.446	0.643
C:N	2.133	0.131	0.007	0.935	0.063	0.939
C:P	1.526	0.229	0.069	0.795	0.017	0.983
N:P	0.075	0.927	0.109	0.743	0.138	0.871

Table 6. *Correlation coefficients of soil and leaf carbon, nitrogen, and phosphorus stoichiometry*

		Leaf					
		C	**N**	**P**	**C:N**	**C:P**	**N:P**
Soil	SOC	0.108	0.008*	-0.019*	0.045*	-0.005*	-0.007*
	TN	0.195	-0.034*	-0.115	0.095	0.11	0.105
	TP	0.188	-0.059	-0.205	0.113	0.216	0.219
	C:N	-.338	0.196	.305	-0.252	-.348	-0.278
	C:P	-0.075	0.038*	0.19	-0.006*	-0.212	-0.25
	N:P	0.21	-0.092	-0.08	0.159	0.087	0.029*

Discussion

Leaf nutrient concentrations can characterize plant nutritional status, which is influenced by environmental factors such as soil properties and water availability. In this study, the mean leaf carbon concentrations (384.29 mg g^{-1}) were lower than the global average in 492 other terrestrial plants (464.00 mg g^{-1}) (Elser et al., 2000) but were higher than that in Zhangjiangkou Mangrove Nature Reserve (345.41 mg g^{-1}) (Fan et al., 2019). These results might be due to the study region having a subtropical monsoon climate, which is hot and humid, and the accumulated plant biomass is higher than that at higher latitudes. Leaf carbon concentrations increased with elevation in the three intertidal zones. The possible reason is that mangrove plants grow in the intertidal zone along the coast and are inundated by seawater at high tide. Inundation conditions decrease the leaf water potential, destroy the chlorophyll structure, and decrease enzyme activity, which reduces the ability to transport the photosynthesis product. Thus, the leaf carbon concentration in the low intertidal zone was lower than that in the high intertidal zone.

The leaf nitrogen and phosphorus concentrations (13.1 and 1.08 mg g^{-1}, respectively) were lower than those in Chinese wetlands (16.07 and 1.85 mg g^{-1}, respectively) (Hu et al., 2014). The reason might be that mangrove plants grow faster at lower latitudes than at higher latitudes, and the biomass accumulation consumes more nitrogen and phosphorus. The leaf nitrogen concentration results were as follows: mid-intertidal zone > low intertidal zone > high intertidal zone. The mid-intertidal zone is at the center of the intertidal zone and is protected from strong winds and waves in addition to human activities. Thus, mangrove plants grow rapidly and synthesize large amounts of protein. The leaf phosphorus concentration was as follows: low intertidal zone > high intertidal

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zone > mid-intertidal zone. The low intertidal zone has deep soil deposits, and the relatively high phosphorus concentration of the soil provides a sufficient source of phosphorus for plants.

The leaf C:N and C:P ratios characterize the plant's ability to assimilate carbon and nutrient utilization and growth rates when absorbing nitrogen and phosphorus. The leaf N:P ratio reflects community-level nutrient limitation patterns (Güsewell et al., 2010; Zhang et al., 2019). In this study, the leaf C:N and C:P ratios (30.31 and 393.02, respectively) were much higher than the global average leaf C:N and C:P ratios (22.50 and 232.00, respectively) (Elser et al., 2000). The leaf N:P ratio indicates the effectiveness of nitrogen and phosphorus supply conditions, which characterizes the environmental nutrient supply for plant growth and the growth rate (Zeng et al., 2013; Hong et al., 2024). The average leaf N:P ratio (12.85) in the study was higher than the average N:P ratio of Chinese wetland plants (8.67). Generally, an N:P ratio < 14 is nitrogen-limited, and a ratio > 16 is phosphorus-limited (Elser et al., 2000). For example, the mean N:P ratio of the two dominant plants in the Poyang Lake wetlands was 21.25, which was mainly limited by phosphorus (Zheng et al., 2013). In this study, the mean leaf N:P ratio was 12.85, indicating that mangrove plant growth in the Beilun River Estuary is nitrogen-limited.

Soil organic carbon is an important soil fertility index (Zhang et al., 2016; Wang et al., 2024). In this study, soil organic carbon concentrations were higher in the high intertidal zone, probably due to the periodic tidal rise and fall bringing in more organic matter. The organic matter renders microbial decomposition more active, resulting in higher soil organic carbon concentrations. The soil organic carbon concentration of the 30–40 cm profile was higher than that of the 0–10 cm profile in the high intertidal zone, probably due to the fact that mangrove plant root systems are mainly distributed below 20 cm. Accordingly, the soil organic carbon concentrations were higher at 30–40 cm than that of the surface soils.

The main nitrogen sources in natural soils are plant and animal residues and biogenic nitrogen fixation, and atmospheric precipitation and flood transport contribute a small amount. The soil nitrogen output is mainly soil organic matter decomposition, most of which is absorbed and utilized by plants. Part of the organic nitrogen is returned to the atmosphere through mineralization (ammonification), nitrification, denitrification, ammonia volatilization, and other biological processes (Reich and Oleksyn, 2004). In this study, the soil nitrogen concentration was lowest in the mid-intertidal zone due to the favorable environment and rapid plant growth that requires more nitrogen from the soil for plant protein synthesis.

Soil phosphorus is mainly derived from rock weathering. Human activities in the high-tidal zone affect the vertical distribution of soil phosphorus concentration. The soil C:N and C:P ratios indicate the soil utilization efficiency of nutrients. The soil N:P ratio indicates soil nutrient availability during plant growth (Zhang et al., 2012; Song et al., 2024). In this study, the C:N, C:P, and N:P ratios were 24.94, 79.77, and 3.41, respectively, where the C:N ratio was higher than the Chinese soil average (13), and the C:P and N:P ratios were lower than the Chinese soil average (105 and 8, respectively) (Tian et al., 2010). This difference might be due to organic matter releasing low nitrogen amounts during soil mineralization, resulting in relatively low N:P ratios.

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Conclusions

This study examined the carbon, nitrogen, and phosphorus concentrations and the C:N, C:P, and N:P ratios along a small-scale intertidal gradient in the mangroves of Beilun Estuary National Nature Reserve. The results confirmed that plant communities and intertidal gradient in the mangrove forest influenced the soil organic carbon, nitrogen, and phosphorus concentrations and stoichiometry. However, the results were based primarily on a field investigation. Thus, further studies are needed to investigate how hydrological conditions influence plant and soil stoichiometry characteristics.

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Conflict of Interest. The authors declare no competing interests.

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