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Article

Leaf Carbon, Nitrogen and Phosphorus Stoichiometry of Three Mangrove Species during Early Establishment after *Spartina alterniflora* Removal

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Abstract: To evaluate the establishment adaptability of mangrove plants during the early restoration stage after *Spartina alterniflora* removal, this study investigated three mangrove species—*Kandelia obovata*, *Aegiceras corniculatum*, and *Avicennia marina*—planted in the Linluandu coastal wetland of Quanzhou Bay following the mechanical removal of *S. alterniflora*. Mature leaves were collected in winter, spring, summer, and autumn of 2024. Leaf total carbon (TC), total nitrogen (TN), and total phosphorus (TP) contents were determined, and the ecological stoichiometric characteristics of C/N, C/P, and N/P were analyzed. The results showed that both season and species had significant effects on leaf TC, TN, and TP contents, as well as their stoichiometric ratios. In *K. obovata*, TC, TN, and TP contents all reached their maximum values in autumn. In *A. corniculatum*, TC content was highest in summer, whereas TN and TP contents peaked in autumn. *A. marina* had the highest seasonal mean TN and TP contents among the three species, at 24.91 g/kg and 2.35 g/kg, respectively, indicating a stronger capacity for nitrogen and phosphorus acquisition. The C/N and C/P ratios followed the order *K. obovata* > *A. corniculatum* > *A. marina*, suggesting relatively higher nutrient-use efficiency in *K. obovata*. The seasonal mean leaf N/P ratios of all three mangrove species were below 14, indicating that plant growth during the early restoration stage was generally limited by nitrogen. Overall, *A. marina* showed the best performance in nitrogen and phosphorus accumulation and nutrient acquisition, and is therefore more suitable as the preferred pioneer species during the early restoration stage after *S. alterniflora* removal. *K. obovata* may serve as a supplementary species in nutrient-poor habitats.

Keywords: *Spartina alterniflora*; Mangrove restoration; Mangrove plants; Ecological stoichiometry; Nitrogen limitation

1. Introduction

Spartina alterniflora is one of the most problematic invasive alien plants in China's coastal wetlands. Through rapid expansion, it can alter tidal-flat vegetation patterns, habitat structure and ecological processes. At the national level, the Special Action Plan for the Prevention and Control of *S. alterniflora* emphasizes scientific control, precise management, ecological restoration and long-term maintenance. Therefore, the effectiveness of vegetation reconstruction after *S. alterniflora* removal has become an important component in evaluating the success of control and restoration practices [1].

During the early restoration stage after *S. alterniflora* removal, whether mangrove plants can establish successfully and eventually form stable communities depends on their growth performance, resource allocation patterns and adaptability to intertidal environments. Mangrove restoration is not simply afforestation; its success is jointly influenced by hydrological connectivity, tidal elevation, sediment conditions, species selection and post-planting monitoring [2]. Restoration design should prioritize the recovery of suitable habitats and, where natural recovery is insufficient, should combine appropriate species planting, post-restoration monitoring and adaptive management to improve restoration success [3]. In areas invaded by *S. alterniflora*, replacement planting and mangrove restoration can promote the decline of invasive herbs and the recovery of native communities through shading, competition and habitat improvement [4]. Invasion and restoration can also alter soil carbon and nitrogen contents and microbial functional traits, including microbial carbon-source utilization patterns [5].

From the perspective of nutrient ecology, leaf C, N and P contents and their stoichiometric characteristics are important indicators for revealing plant nutrient acquisition, allocation and use efficiency. Mangrove plants commonly grow in nutrient-limited environments, and different species show marked differences in N and P conservation and utilization strategies [6]. Therefore, this study focused on *Kandelia obovata*, *Aegiceras corniculatum* and *Avicennia marina* planted after mechanical removal of *S.*

alterniflora in the Linluandu area of Quanzhou Bay. By comparing leaf C, N and P contents and ecological stoichiometric traits among the three species, this study aimed to identify suitable mangrove species for the early restoration stage and to provide a scientific basis for mangrove restoration and subsequent management of invaded tidal flats.

2. Materials and Methods

2.1. Study Area and Sample Processing

Quanzhou Bay is located in southeastern Fujian Province, China, and is the estuarine confluence area of the Jinjiang and Luoyang rivers. It is also an important bay in Quanzhou City. The geomorphology of the region is dominated by estuarine landforms and muddy coasts, with an average elevation of approximately 0.8 m. The soils mainly include coastal saline soil, fluvo-aquic soil and aeolian sandy soil.The experimental site was located in the Linluandu coastal wetland in the northeastern part of Hanjiang Town, Shishi City, on the southern shore of Quanzhou Bay (24°47′49″ N, 118°42′54″ E) (Figure 1). According to the planted mangrove species, the experimental site was divided into three zones: the mechanical tillage + *K. obovata* planting zone (QG), the mechanical tillage + *A. corniculatum* planting zone (TG), and the mechanical tillage + *A. marina* planting zone (BG). After mangrove planting was completed, field sampling was conducted four times in 2024, namely in January (winter), April (spring), July (summer) and October (autumn).

Three sampling stations were established in each planting zone, and three parallel 2 m × 2 m quadrats were set at each station. In each quadrat, relatively mature and stable leaves were randomly collected from five plants and sealed in self-sealing bags. Leaf total carbon (TC) and total nitrogen (TN) contents were determined using a FLASH SMART elemental analyzer (Thermo Fisher, USA). Leaf total phosphorus (TP) content was determined using an iFIA7 automatic flow injection analyzer (Titan Instruments, China).

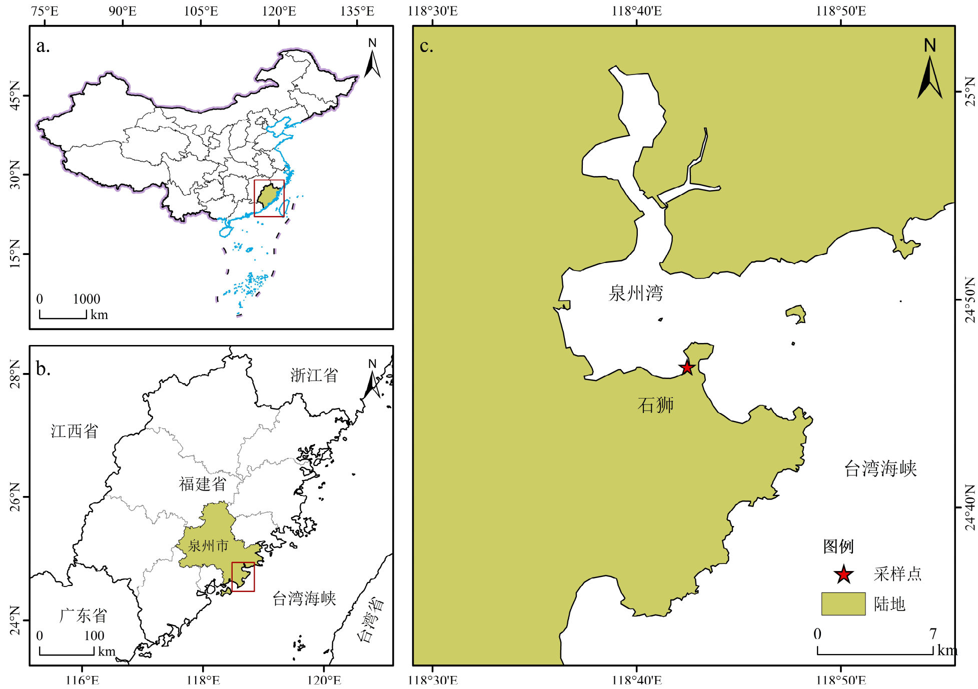


Fig. 1. The environment and sampling sites of the Quanzhou Bay, Fujian Province, China.

2.2. Data Analysis

Raw data were first preprocessed in Microsoft Excel 2019. The mean and standard deviation of each indicator were calculated based on three replicate samples. Statistical analyses were performed using SPSS Statistics 24.0. Two-way analysis of variance (two-way ANOVA) was used to examine the effects of sampling season and plant species on C, N and P contents and their stoichiometric ratios. One-way analysis of variance (one-way ANOVA) was used to test differences among groups, followed by the S-N-K method for post hoc multiple comparisons. Statistical significance was set at $p < 0.05$, with $p < 0.01$ and $p < 0.001$ indicating higher significance levels. Figures were produced using Origin 2024.

3. Results

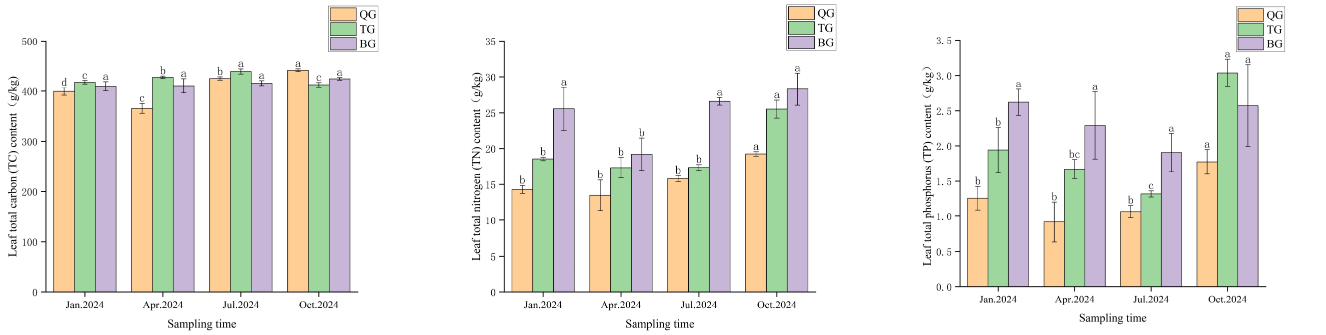
3.1. Seasonal Dynamics of Leaf C, N and P Contents in the Three Mangrove Species

The two-way ANOVA results for leaf C, N and P nutrient traits showed that both season and plant species had highly significant effects on leaf TC, TN and TP contents ($p < 0.001$). The interaction between season and plant species had highly significant effects on TC and TN contents ($p < 0.001$ and $p < 0.01$, respectively), and a significant effect on TP content ($p < 0.05$).

In *K. obovata*, leaf TC content followed the seasonal pattern autumn (441.78 ± 2.77 g/kg) > summer (425.29 ± 3.26 g/kg) > winter (399.44 ± 7.53 g/kg) > spring (365.97 ± 9.63 g/kg), with significant differences among seasons ($p < 0.05$). In *A. corniculatum*, TC content was highest in summer (439.28 ± 5.17 g/kg), significantly higher than in the other seasons ($p < 0.05$). In *A. marina*, TC content was highest in autumn (424.54 ± 2.66 g/kg). Based on seasonal means, leaf TC content followed the order *A. corniculatum* (424.33 ± 11.19 g/kg) > *A. marina* (415.22 ± 9.69 g/kg) > *K. obovata* (408.12 ± 30.41 g/kg).

In *K. obovata*, leaf TN content was significantly higher in autumn (19.26 ± 0.31 g/kg) than in the other seasons ($p < 0.05$). In *A. corniculatum*, TN content was also significantly higher in autumn (25.51 ± 1.24 g/kg) than in the other seasons ($p < 0.05$). In *A. marina*, TN content reached its maximum in autumn (28.29 ± 2.24 g/kg), whereas spring values were significantly lower than those in the other seasons ($p < 0.05$). Based on seasonal means, leaf TN content followed the order *A. marina* (24.91 ± 4.05 g/kg) > *A. corniculatum* (19.69 ± 3.64 g/kg) > *K. obovata* (15.71 ± 2.50 g/kg).

In *K. obovata*, leaf TP content was significantly higher in autumn (1.78 ± 0.17 g/kg) than in the other seasons ($p < 0.05$). In *A. corniculatum*, TP content was also significantly higher in autumn (3.04 ± 0.19 g/kg) than in the other seasons ($p < 0.05$). In *A. marina*, TP content followed the seasonal pattern winter (2.62 ± 0.19 g/kg) > autumn (2.57 ± 0.58 g/kg) > spring (2.29 ± 0.48 g/kg) > summer (1.91 ± 0.27 g/kg), with no significant differences among seasons ($p > 0.05$). Based on seasonal means, leaf TP content followed the order *A. marina* (2.35 ± 0.46 g/kg) > *A. corniculatum* (1.99 ± 0.69 g/kg) > *K. obovata* (1.25 ± 0.38 g/kg).



(**a**) (**b**) (**c**)

Fig. 2. (**a**) Seasonal variation of leaf total carbon content from Jan. to Oct. 2024; (**b**) Seasonal variation of leaf total nitrogen content from Jan. to Oct. 2024; (**c**) Seasonal variation of leaf total phosphorus content from Jan. to Oct. 2024.

3.2. Seasonal Dynamics of Leaf C, N and P Ecological Stoichiometry in the Three Mangrove Species

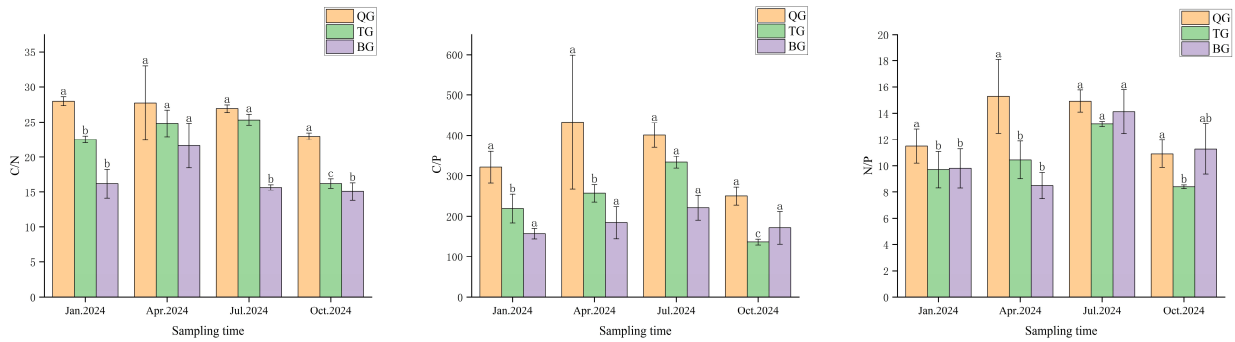
The two-way ANOVA results for leaf ecological stoichiometric traits showed that season and plant species had highly significant effects on C/N, C/P and N/P ratios ($p < 0.001$). The interaction between season and plant species significantly affected C/N and N/P ratios, whereas its effect on C/P was not significant.

In *K. obovata*, the C/N ratio was highest in winter (27.97 ± 0.61), with no significant differences among seasons ($p > 0.05$). In *A. corniculatum*, the C/N ratio followed the seasonal pattern summer (25.31 ± 0.79) > spring (24.78 ± 1.90) > winter (22.51 ± 0.48) > autumn (16.19 ± 0.65), reaching its maximum in summer and decreasing significantly in autumn. In *A. marina*, the C/N ratio was significantly higher in spring (21.63 ± 3.16) than in the other seasons ($p < 0.05$).

In *K. obovata*, the C/P ratio was highest in spring (433.38 ± 165.63), with no significant differences among seasons ($p > 0.05$). In *A. corniculatum*, the C/P ratio followed the pattern summer (333.96 ± 14.92) > spring (256.94 ± 21.34) > winter (219.04 ± 35.41) > autumn (136.23 ± 7.68), peaking in summer and decreasing significantly in autumn. In *A. marina*, the C/P ratio was highest in summer (221.10 ± 30.67), with no significant differences among seasons ($p > 0.05$).

In *K. obovata*, the N/P ratio was highest in spring (15.28 ± 2.81), with no significant differences among seasons ($p > 0.05$). In *A. corniculatum*, the N/P ratio was significantly higher in summer (13.19 ± 0.20) than in the other seasons ($p < 0.05$). In *A. marina*, the N/P ratio was highest in summer (14.11 ± 1.66), significantly higher than those in winter and spring ($p < 0.05$).

Based on seasonal means, both C/N and C/P ratios followed the order *K. obovata* (26.38 ± 3.12 and 351.69 ± 105.23, respectively) > *A. corniculatum* (22.20 ± 3.90 and 236.54 ± 76.76, respectively) > *A. marina* (17.13 ± 3.23 and 183.47 ± 37.52, respectively). The N/P ratio followed the order *K. obovata* (13.15 ± 2.50) > *A. marina* (10.92 ± 2.55) > *A. corniculatum* (10.44 ± 2.02).



(a) (b) (c)

Fig.3. Seasonal dynamics of leaf C/N, C/P and N/P stoichiometric ratios in three mangrove species *(Kandelia obovata, Aegiceras corniculatum* and *Avicennia marina*) from January to October 2024. (**a**) Leaf carbon to nitrogen (C/N) ratio; (**b**) Leaf carbon to phosphorus (C/P) ratiol; (**c**) Leaf nitrogen to phosphorus (N/P) ratio.

4. Discussion

Carbon, nitrogen and phosphorus are essential elements for plant growth and development. Their contents in leaves and their ecological stoichiometric characteristics can reflect plant nutrient absorption and utilization patterns, environmental adaptability and potential nutrient limitation. The results of this study showed that seasonal variation and plant species jointly drove the dynamics of leaf carbon (TC), nitrogen (TN) and phosphorus (TP) contents in the three mangrove species. Both season and species had dominant effects on TC, TN and TP contents, and their interaction also significantly regulated TC and TN contents, with a certain effect on TP content. Meanwhile, leaf C/N, C/P and N/P stoichiometric ratios were also jointly controlled by seasonal variation and species identity. These findings indicate that, during the establishment of mangrove plants in tidal flats previously invaded by *S. alterniflora*, leaf nutrient accumulation and stoichiometric traits were strongly regulated by seasonal environmental variation and also showed clear species-specific patterns. These patterns are likely the result of interactions between plant growth rhythms and environmental nutrient availability, while stoichiometric homeostasis may buffer plants against environmental fluctuations [7].

In *K. obovata*, leaf TC, TN and TP contents all reached their highest values in autumn, while TN and TP contents in *A. corniculatum* and *A. marina* also peaked in autumn. The increase in leaf C, N and P contents in autumn may be associated with nutrient resorption and retranslocation before leaf senescence during the late growing season, which allows plants to conserve internal nutrients, enhance overwintering stress resistance and support growth in the following season [8]. In addition, eddy covariance observations have shown that gross primary productivity (GPP) in mangrove ecosystems can exhibit a "double-peak and single-trough" seasonal pattern, with autumn representing one of the annual productivity peaks [9]. This indicates that mangroves can still maintain high photosynthetic carbon fixation in autumn, thereby facilitating the synchronous accumulation of leaf carbon, nitrogen and phosphorus.

In *A. corniculatum*, leaf TC content reached its maximum in summer (439.28 ± 5.17 g/kg), consistent with the simultaneous summer peaks in canopy width and leaf area. Adequate light and suitable temperature in summer may significantly enhance the net photosynthetic rate and light-use efficiency of *A. corniculatum* [10], thereby improving leaf carbon fixation and promoting the rapid synthesis and accumulation of carbohydrates. This may explain the summer advantage of *A. corniculatum* in both chemical composition and morphological development.

Among the three species, *A. marina* had significantly higher seasonal mean TN and TP contents than *A. corniculatum* and *K. obovata*. This pattern was consistent with its relatively rapid growth rate. According to the growth rate hypothesis proposed by Sterner and Elser [11], fast-growing species generally require higher N and P contents to support ribosome synthesis, protein turnover and other physiological processes associated with rapid growth. As a pioneer species in the intertidal zone, *A. marina* is adapted to rapid establishment and population expansion on newly exposed tidal flats after *S. alterniflora* removal. This adaptation is closely related to its distinctive nitrogen acquisition mechanism [12]. *A. marina* can actively acquire atmospheric nitrogen through diazotrophic nitrogen fixation associated with its aerial roots, enabling it to accumulate nutrients more efficiently in low-nitrogen tidal-flat habitats. Consequently, its leaf N and P levels were relatively high, indicating a nutrient-use strategy characterized by active nutrient acquisition to support rapid growth.

In contrast, *K. obovata* showed relatively low leaf N and P contents, while its C/N and C/P ratios were significantly higher than those of *A. corniculatum* and *A. marina*. This suggests that *K. obovata* has higher nutrient-use efficiency and can maintain growth under low nutrient availability through efficient nutrient cycling. This represents an important adaptive strategy for nutrient-poor intertidal habitats [13]. Therefore, *K. obovata* may be suitable for replacing *S. alterniflora* in areas with relatively low nutrient availability.

C, N and P contents are core indicators of plant nutritional stoichiometry, and their contents and ratios (C/N, C/P and N/P) provide key information for quantifying plant nutrient use and environmental responses in coastal wetland ecosystems. In this study, the interaction between season and species significantly affected C/N and N/P ratios, but not C/P. This indicates that seasonal variation in leaf C/P was more consistent among species and was mainly regulated by overall seasonal environmental changes, whereas C/N and N/P were jointly influenced by species-specific nutrient-use strategies and seasonal variation. This finding is consistent with global patterns of leaf stoichiometry in coastal wetlands, where different stoichiometric ratios are controlled by different factors [14].

From a seasonal perspective, the C/N and C/P ratios of the three mangrove species generally tended to be lower in summer and autumn than in winter and spring. Mangroves commonly grow in N- and P-limited intertidal environments [15]. During summer and autumn, which are the main growing seasons for mangrove plants, the demand for N, P and other essential nutrients increases markedly. Plants preferentially allocate absorbed nutrients to leaves, resulting in higher leaf N and P concentrations and consequently lower C/N and C/P ratios. For example, studies on *K. obovata* along the southeastern coast of China have shown seasonal variations in leaf N and P contents and nutrient resorption strategies [13]. Meanwhile, during the non-growing season, plant growth rate and metabolic intensity decline, and demand for N and P decreases. Photosynthetically produced sugars and other nonstructural carbohydrates are more likely to be stored within plant tissues, contributing to increases in C/N and C/P ratios [16].

According to the nutrient limitation threshold proposed by Koerselman and Meuleman [17], plant growth is mainly limited by nitrogen when leaf $N/P < 14$, co-limited by nitrogen and phosphorus when $14 < N/P < 16$, and mainly limited by phosphorus when $N/P > 16$. In this study, the seasonal mean N/P ratios of the three mangrove species ranged from 10.44 to 13.15, all below the threshold of 14. This indicates that the growth of the three mangrove species during the early establishment stage in the *S. alterniflora*-invaded tidal flat of Quanzhou Bay was primarily limited by nitrogen. Previous studies have also suggested that soils in China's coastal wetlands are commonly characterized by nitrogen limitation [18]. The N/P ratios of *A. corniculatum* and *A. marina* reached their annual maxima in summer, suggesting that nitrogen demand increased substantially during the summer growing season and that nitrogen limitation became more pronounced. These results provide practical guidance for mangrove restoration in *S. alterniflora*-invaded tidal flats of Quanzhou Bay. During the early establishment stage, moderate application of slow-release nitrogen fertilizer may help alleviate nitrogen limitation and improve plant growth and restoration efficiency, which is consistent with previous findings on soil nutrients in mangrove wetlands [19].

5. Conclusions

Leaf TC, TN, and TP contents, as well as C/N, C/P, and N/P ratios, showed significant seasonal and interspecific differences. *Avicennia marina* had the highest mean TN and TP contents, indicating a strong nutrient acquisition capacity, whereas the relatively high C/N and C/P ratios of *Kandelia obovata* reflected higher nutrient-use efficiency. The seasonal mean leaf N/P ratios of all three species were below 14, suggesting that the three mangrove species were generally nitrogen-limited during the early restoration stage in the study area. Therefore, moderate nitrogen supplementation may be considered in subsequent management to alleviate nitrogen limitation and promote mangrove growth. Overall, *A. marina* is the most recommended pioneer species among the three mangrove species.

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Data Availability Statement: The original data in this study were obtained through the research and analysis conducted by the authors. If necessary, it can be provided by contacting the corresponding author.

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