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Periodic Flooding Decoupled the Relations of Soil C, N, P, and K Ecological Stoichiometry in a Coastal Shelterbelt Forest of Eastern China

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Abstract: Understanding the variation in soil nutrients found in coastal shelterbelt forests in response to periodic flooding is crucial for restoring the soil quality of flooded stands. In this study, we examined soil organic carbon (SOC), total nitrogen (TN), total phosphorus (TP), total potassium (TK) contents and their ecological stoichiometry, as well as soil organic matter and soil-available N, P, and K contents at three soil depths (0–10, 10–20 and 20–30 cm), in a shelterbelt forest of eastern China that was affected by periodic flooding. Results showed that soil C, N, and P contents all had a clear decreasing trend after being flooded, with significant decreases in SOC, TN and hydrolyzable N of 0–10 cm soil, as well as TP of 10–20 cm soil. Soil K content, however, had minimal changes after flooding across different soil layers. Soil C:N ratio increased significantly in 0–10 cm layer, while soil C:P, C:K, N:P, N:K, and P:K ratios decreased notably in both 0–10 cm and 20–30 cm layers following the flooding. Additionally, periodic flooding partially decoupled the correlations among SOC, TN, TP, TK and their ratios. For example, the connection between TK and N:P reversed into a negative correlation in 10–20 cm soil, while SOC and TK became negatively correlated with TP and P:K in the 20–30 cm layer. Principal component analysis revealed the effects of periodic flooding on soil C, N, P, and K availability, in which the total explained variance was decreased from 94% to 86.6%. Specifically, flooding significantly reduced the SOC and soil TN contents on the first axis, influencing C- and N-related ratios. On the second axis, flooding mainly affected soil TK content, which subsequently influenced the correlation between SOC and TK. Thus, periodic flooding notably affected the soil C, N, P, and K ecological stoichiometries of the coastal forest, but the variation patterns were depth-dependent. The insights gained from these results can contribute to the restoration of soil quality in degraded stands caused by flooding in the coastal shelterbelts regions of Eastern China.

Keywords: soil nutrients; soil depths; ecological stoichiometry; SOC

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Citation: Bao, B.; Chang, M.; Jin, S.; Li, X.; Xie, H. Periodic Flooding Decoupled the Relations of Soil C, N, P, and K Ecological Stoichiometry in a Coastal Shelterbelt Forest of Eastern China. *Forests* **2023**, *14*, 2270. https://doi.org/10.3390/f14112270

Academic Editor: Steven McNulty

Received: 30 September 2023
Revised: 11 November 2023
Accepted: 14 November 2023
Published: 20 November 2023

1. Introduction

Coastal shelterbelt forests serve critical ecofunctions in resisting natural disasters, assisting in windbreak, sand fixation, and water conservation [1]. They also enhance the ecosystem services of coastal zones, which is crucial to improving the living conditions of coastal residents and promoting regional economies. However, these forests are susceptible to damage from typhoon, storm surge, strong wind, salinity, and other disturbances [2,3]. Flood also occurs in coastal shelterbelt forests. For instance, in a rainstorm weather, excessive rainfall can lead to flooding [4]. Besides, the backflow of seawater can also cause flooding beyond some rivers of the seashore regions [5]. The duration of natural flooding usually lasts for two to five days in a coastal shelterbelt forest, depending on the amount of rainfall and air temperature during the period. Flooding has been found to have significant impacts on the physical and chemical properties of soil [6,7]. The flooded soil generally lacks oxygen, leading to reduced soil respiration and soil redox potential [8]. The redox conditions of soil have an impact on the rates of nutrient absorption and release, which in turn affects the soil nutrient contents and alters the cycling of major nutrients [9]. Additionally, the temporal dynamics of soil nutrients in relation to periodic flooding have also been reported by many previous studies, but the results varied in terms of experimental scales and the duration of flooding [10,11].

Carbon (C), nitrogen (N), and phosphorus (P) are the primary soil nutrients and play significant roles in various physiological and ecological processes within plant–soil systems [12,13]. While ecological stoichiometry is widely used to study the quantitative relationships among elements in ecological processes, as well as to estimate nutrient limitation state and assess the balance of multiple nutrient elements [14,15], evaluating soil nutrient contents and their stoichiometry can provide further insights into the mechanisms of nutrient cycling and balance in various ecosystems [16]. Many studies have also highlighted the importance of potassium (K) in soil elemental composition, but the ratios between K and other elements can be greatly influenced by environmental factors [17,18]. Since K can be easily leached from soil during flooding, with water-soluble K being particularly susceptible [19,20], Alfaro et al. (2004) [21] found that the leached K in sandy soils could exceed 70 $kg \cdot ha^{-1}$ under high rainfall intensity, which had already surpassed the rate of K input during the same period. The authors also found that such heavy leaching could further aggravate K deficiency in many regions [22]. However, studies on stoichiometric relationships between soil K and other nutrient elements under flooded conditions are still inadequate [21,23].

In terrestrial ecosystems, the largest pools of C, N, P, and K are stored in soils, but they are at a risk of being released due to growing soil disturbances, such as land use change, soil pollution and flooding [24,25]. Soil P and K contents are influenced by factors such as parent material, soil development stage, weathering, and erosion intensity [26,27]. However, flooding can cause soil slaking and structure disaggregation, leading to entrapped air loss and potential changes in the release rates of P and K under flooding conditions [28,29]. Generally, the anaerobic soil environment can decrease soil microbial activity and increase soil organic stabilization [8,30]. However, the seasonal aerobic and anaerobic conditions also have considerable effects on the soil mineralization and the nutrient dynamic in riparian areas [31,32]. In grassland, flooding actually increased the decomposition of soil organic carbon [33]. These inconsistent findings may be attributed to the variations in soil types and flooding intensities. For instance, in riparian zones of the Hulunbuir steppe, soil C:N ratio remained relatively stable, while soil N:P and C:P ratios showed significant changes under different submergence frequencies [34]. Despite poor stand condition and frequent disturbances in coastal habitats, few studies have quantified the ecological stoichiometry of soil nutrients affected by flooding in coastal shelterbelt forests [35]. However, more complicated relationships between C, N, P, and K could be expected in these forests due to their specific habitat characteristics [36].

Soil depth also plays a critical role in the distribution pattern of C, N, P, and K contents in different ecosystem components [37]. Previous studies have explored the spatial heterogeneity of soil nutrients and the ecological stoichiometry in terrestrial ecosystems and soil profiles [38]. In the grasslands of northern China, soil C and N contents tended to decrease with increasing soil depth, while soil P content did not differ [19]. However, the effects of periodic flooding on soil nutrient contents and their stoichiometry with different soil depths in coastal forests remain understudied. Therefore, we conducted a field experiment in the eastern Zhejiang province of China to evaluate the soil C, N, P, and K contents and their stoichiometry in a shelterbelt forest to determine how seriously they were affected by the periodic flooding caused by tides. Specifically, the following hypotheses were tested: (1) soil C, N, P, and K contents would be reduced after being flooded due to leaching; (2) deeper soil would be less impacted by flood since weaker erosion; (3) and flooding would decouple the correlations between C, N, P, and K stoichiometry as periodic disturbance might not provide enough time to achieve an element balance.

2. Material and Methods

2.1. Study Area

The study was conducted in the coastal shelterbelt forests of Xiangshan County, Ningbo City, Zhejiang Province (28°51′28″ N, 121°34′15″ E). Xiangshan County has an 800 km long coastline with infertile soil, characterized by high salinity ranging from 1.2‰ to 3.5‰ and a pH of approximately 8.0 [39]. The main tree species in coastal forests include *Casuarina equisetifolia*, *Sapium sebiferum*, and *Nerium indicum*, etc. The average annual temperature and precipitation are 16.6 °C and 1450 mm, respectively. The study area experiences a subtropical monsoon climate, making it susceptible to subtropical high pressure and airflow in summer days, as well as abnormal weather phenomena such as typhoons and rainstorms [40]. Adjacent to the experimental forestbelt is a canal connected to the East China Sea. During high-tide period, seawater surges into the canal, while during the spring tides the river rises and overflows, causing flooding in parts of the forestbelts. Consequently, the experimental site is periodically affected by seawater flooding. The spring tide occurs twice a month, resulting in the flooding of forestbelts, which usually lasts for two to five days per time, depending on the amount of rainfall and the temperature at the time.

2.2. Experimental Design, Sample Collection and Chemical Analysis

The experimental stands were taken from 10-year-old *C. equisetifolia* plantations with a belt width of 30–50 m. Six stands were randomly selected in the flooded area. In August 2021, a 2 m × 2 m plot was set up in each stand center, while other 6 plots were randomly set up in the normal, non-flooded stands to serve as the control. The control plots were positioned at least 30 m away from the flooded plots to prevent any possible seepage from the seawater. Since the flooded plots went through periodic flooding, with a duration of 3 days for flooding and 12 days for drying on average in a spring tide cycle, we collected the soil samples 10 days after the flooding to approximate the moisture level of the non-flooded soil as much as possible. Within each plot, three sampling points were selected using the diagonal sampling method. At each sampling point, a stainless soil auger with a diameter of 5 cm was used to collect soil samples from three different layers, 0–10, 10–20, and 20–30 cm, for inclusion in the chemical analysis. The soil samples were thoroughly mixed into a composite sample for each layer in each plot. Subsequently, all the samples were transported to the laboratory, air-dried at room temperature, and sieved through a 2 mm mesh before undergoing chemical analysis. The SOC content was measured using the potassium dichromate oxidation–external heating method. Soil total N was estimated using a semi-micro-Kjeldahl technique [41]. Following the calcination of the soil sample at 550 °C [42], total P was analyzed using sulfuric acid-soluble Mo–Sb colorimetry after solution extraction using sulfuric acid. Soil total K was analyzed using sodium hydroxide alkali fusion–flame photometry [43]. Soil-hydrolyzable N was quantified using alkaline hydrolysis–diffusion absorption [44]. Soil-available P was extracted and measured using hydrochloric acid–ammonium fluoride. Soil-available K was measured using ammonium acetate extraction–flame photometry [45].

2.3. Data Analysis

A general linear model (GLM) was used to compare the differences in SOC, soil N, P, K contents and their ecological stoichiometric characteristics, as well as soil organic matter and soil-available N, P, and K contents in soils of different depths, with soil depth as the fixed factor and plot as the random factor. The paired-sample *t*-test was employed to compare the differences in soil parameters between the flooded and normal plots. Some of these variables were log-transformed or square root-transformed to meet the requirement of normal distribution. Spearman's correlation analysis was conducted to investigate the relationships between SOC, soil N, P, and K contents and their ecological stoichiometries in flooded and normal soils of different soil layers. Additionally, principal component analysis (PCA) was utilized to determine the main factors controlling changes in SOC, soil

N, P, and K ecological stoichiometries. Statistical analysis and plotting were performed using SPSS 20.0 (IBM, Armonk, NY, USA, USA) and Origin 9.1 (Origin Lab, Northampton, MA, USA), with the significance level set at $p < 0.05$.

3. Results

3.1. Effects of Periodic Flooding on SOC and Soil N, P, and K Contents

The effects of periodic flooding on SOC, soil N, P, and K content vary with soil depth. In 0–10 cm soil layers, significant differences were observed between the flooded and normal soil in terms of SOC, TN, organic matter, and hydrolytic nitrogen content. Organic matter and SOC content decreased by 21.3%, TN content decreased by 26.1%, and hydrolytic nitrogen content decreased by 34.2% under the stress of flooding. Soil TK content increased by 1.24% after being flooded, but the difference was not significantly different the normal soil. In 10–20 cm layers, soil TP content significantly decreased after being flooded. The variation in soil TK content after being flooded was significantly lower than that of soil N and P, and there was no significant difference compared to the normal soil. In 20–30 cm soil layers, there was no significant difference in SOC, N, P, and K content between the flooded soil and normal soil. SOC and TN content decreased with increasing soil depth, and significant differences were observed in organic matter, SOC, and TN in different soil layers after being flooded. There were no significant differences in terms of available P and available K between different soil layers before and after being flooded (Figures 1 and 2).

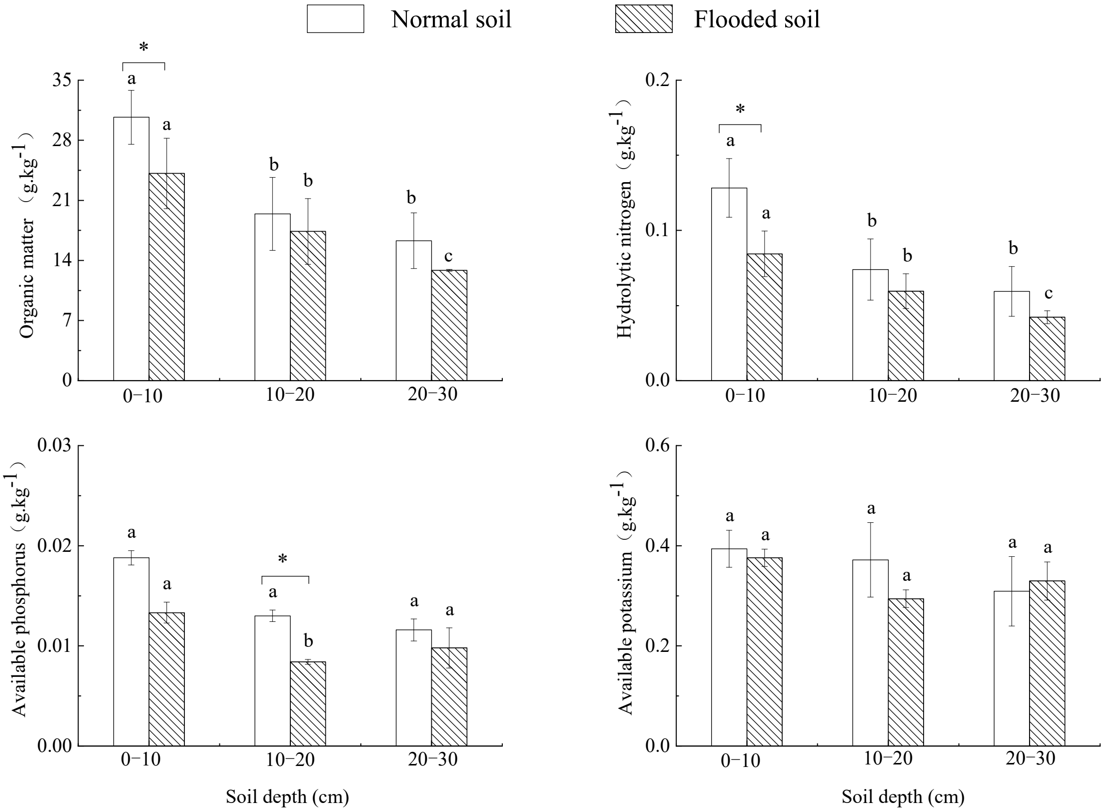

Figure 1. Effect of periodic flooding on SOC, soil N, P, and K contents of coastal shelterbelt forests. Data are mean ± SD (n = 6). An asterisk (*) indicates significant differences between normal and flooded soils at a significance level of $p < 0.05$. Different letters are used to indicate significant differences among soil layers at a significance level of $p < 0.05$.

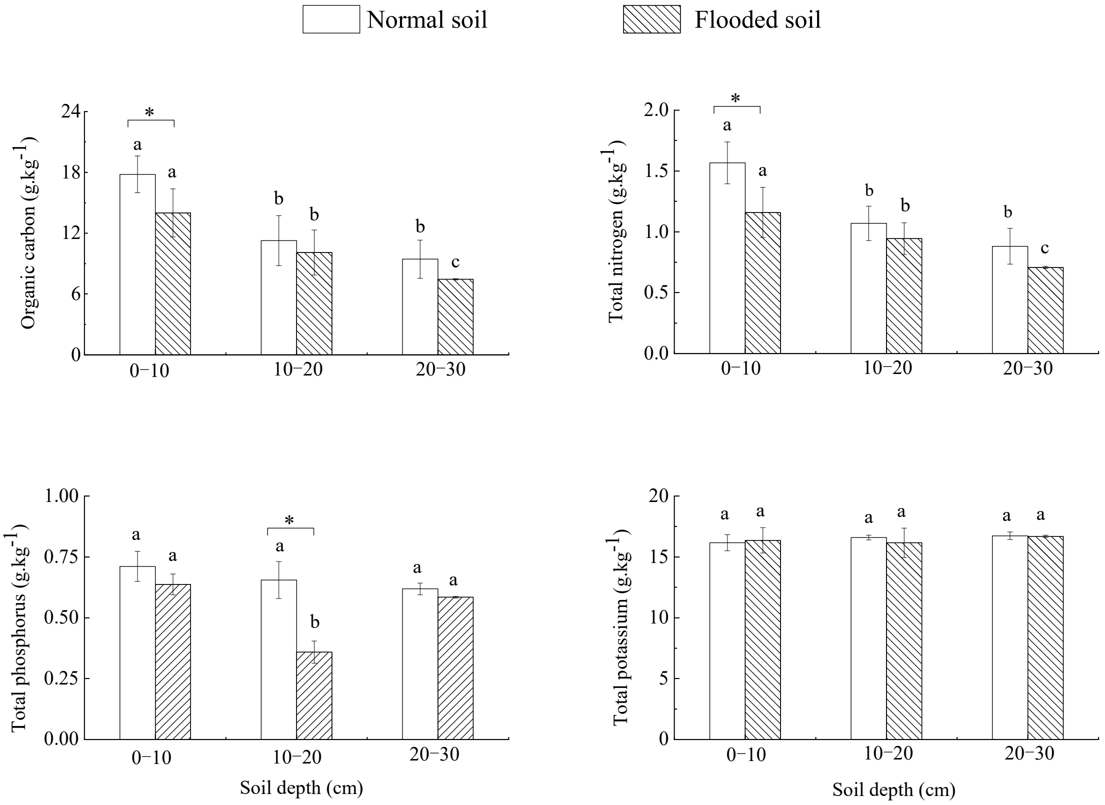

Figure 2. Effect of periodic flooding on the soil organic matter and hydrolytic nitrogen, available phosphorus and available potassium contents of coastal shelterbelt forests. Data are mean ± SD (n = 6). An asterisk (*) indicates significant differences between normal and flooded soils at a significance level of $p < 0.05$. Different letters are used to indicate significant differences among soil layers at a significance level of $p < 0.05$.

3.2. Effects of Periodic Flooding on Soil C:N:P:K Stoichiometries

Periodic flooding had remarkable effects on the ecological stoichiometries of soil C:N:P:K. In 0–10 cm soil layer, C:P, C:K, N:P, N:K, and P:K ratios all decreased significantly after being flooded, while the C:N ratio significantly increased. The ecological stoichiometric ratios of 10–20 cm soil layer were relatively rarely changed. In 20–30 cm soil layer, the flood led to a significant reduction in all the ecological stoichiometric ratios, except for C:N (Figure 3).

3.3. Effect of Periodic Flooding on Correlations of Soil C, N, P, and K Stoichiometries

The correlations between soil C, N, P, and K contents and their stoichiometric ratios varied with soil layers in both normal and the flooded soils. In 0–10 cm soil layers, there was a significant positive correlation between TN and SOC, TP, TK, N:P, and N:K. Additionally, SOC showed a significant positive correlation with C:P, C:K, N:P, and N:K. In 10–20 cm soil layers, there was a significant negative correlation between TK and N:P, but significant positive correlations between SOC and TN, C:N, C:K, and P:K. Furthermore, TN shows a significant positive correlation with C:N, C:K, and P:K in this layer. In 20–30 cm soil layers, SOC was significantly negatively correlated with TP, N:K, and P:K, respectively. TN was negatively correlated with C:N and C:K. TP was significantly negatively correlated with C:N and C:P. Finally, TK was significantly negatively correlated with P:K (Figure 4).

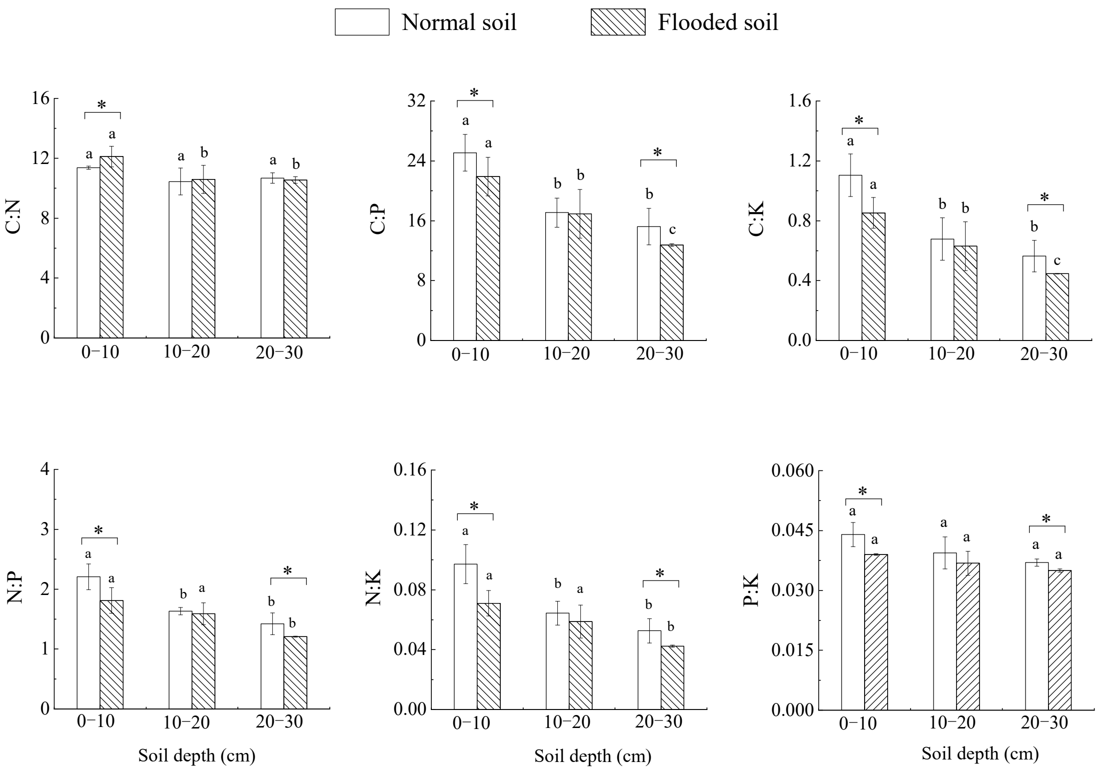

Figure 3. Effect of periodic flooding on soil C:N:P:K in coastal shelterbelt forests. Data are mean ± SD (n = 6). An asterisk (*) indicates significant differences between normal and flooded soils at a significance level of $p < 0.05$. Different letters are used to indicate significant differences among soil layers at a significance level of $p < 0.05$.

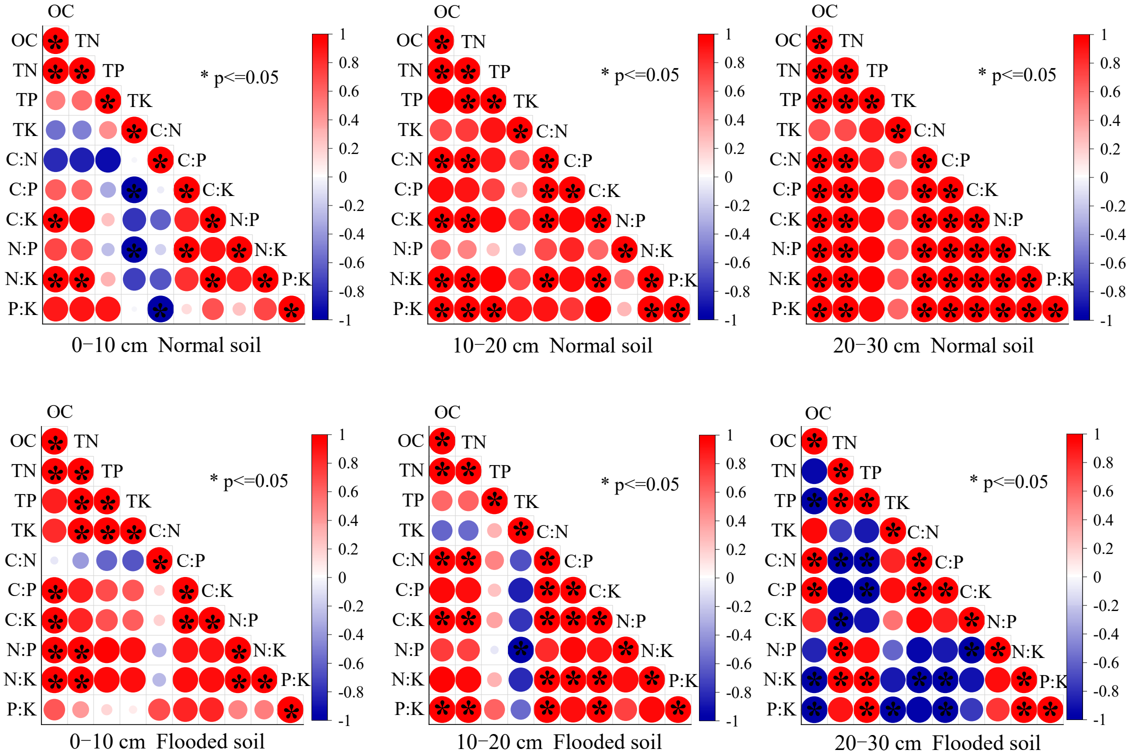

Figure 4. Correlations between SOC, soil N, P and K contents and their stoichiometric ratios in coastal shelterbelt forests in normal and flooded soil (n = 6).

3.4. Soil C, N, P, and K Stoichiometries as Affected by Periodic Flooding

PCA was conducted on SOC, soil N, P, and K contents and their stoichiometric ratios before and after flooding. The results showed that PC 1 and PC 2 explained 94% and 86.6% of the observed variances under normal and flooded conditions, respectively. Under PC1, flooding significantly reduced the content of SOC and soil TN, thus affecting C:N and other stoichiometric characteristics. Under PC2, periodic mainly affected soil TK content, which subsequently influenced the correlation between SOC and TK. Before being flooded, there was a significant negative correlation between SOC and TK, but no significant correlation was observed after the flood (Figure 5).

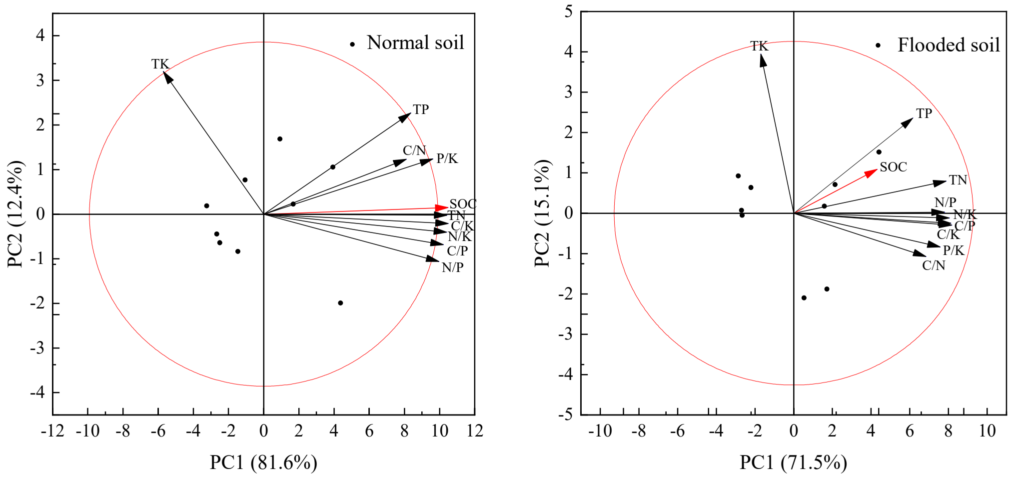

Figure 5. Principal component analysis of SOC, N, P, and K contents and stoichiometric ratios in normal and flooded soils of coastal shelterbelt forests.

4. Discussion

4.1. Effects of Periodic Flooding on Soil C, N, P, and K Contents

The contents of SOC, TN, and TP in flooded soil significantly decreased compared to the normal soil, but these changes were dependent on soil depth. SOC and TN contents declined with the increasing soil depth, which was due to the fact that the surface soil primarily received organic matter inputs from sources such as plant litter and root exudates. As a result, the surface layers contained more nutrients than the deeper layers [46,47]. Our findings indicated that the content of SOC and TN in normal soil was significantly higher than that of the flooded soil. Previous studies have attributed the significant difference in SOC and TN contents between normal and flooded soil to variations in water content and the release of N in easily accessible forms [48,49]. Since flooding led to higher water content and reduced oxygen availability for soil microbes, in order to avoid cell death, microbial activity utilized SOC for denitrification [50,51]. However, in this study, denitrification was unlikely to be responsible for the decline in soil C and N contents in flooded soil because the denitrification rate was extremely low (7 mg C/kg/year), and it would take several hundred years to fully denitrify the soil NO3-N in coastal forests [52,53]. In the 0–10 cm soil layers of our study, we observed a significant reduction in the levels of SOC and TN in flooded soil, which was most likely due to the surface runoff. On one hand, the flow of seawater washed away a portion of litter, while on the other hand, the wetted soil would delay the litter decomposition [54]. As a result, less C and N were released within the flooded stands.

Soil TP content in normal stands remained relatively stable across different soil depths. However, in flooded soil, there was a notable difference in TP content between 10–20 cm and other soil layers. Effective P is not sensitive to environmental changes, thus P in flooded soil is generally lost in the form of particles or dissolved forms through runoff. However, in the surface soil, plants required P to resist the stress caused by flooding and sustain their growth. This led to a rhizosphere enrichment effect, resulting in a significantly higher P content in the surface soil of the flooded stands compared to 10–20 cm soil layers [55,56]. The minimal loss of TP content in the deep soil could be attributed to the influence of soil properties of the coastal forest, factors such as the overall nutrient deficiency, increased soil compaction, and enhanced soil P fixation ability, which make it hard for P to be leached or eroded in the deep soil layer [51,57].

K is primarily absorbed by plants in an ionic form. However, the mobility of these ions makes K more susceptible to erosion, including runoff water and strong wind [20,58]. It is also highly soluble, which means it can be leached to either deeper soil layers or surface waters [59]. Previous studies have indicated that soil K content could be greatly influenced by abiotic factors such as temperature and moisture, etc. [37,60–62]. However, we observed limited variation in TK content in flooded soil compared to the normal soil in this study, with only a slight increase of K in 0–10 cm soil. This was likely due to the offsetting effect of K erosion caused by seawater runoff and strong winds at the experimental sites, which neutralized most of the high K content input from seawater. The repeated flooding resulted in compacted soil, making it challenging for K from seawater to effectively enter the soil [63,64]. Additionally, the available K accounted for only a small fraction of the TK content, and the loss of K through leaching was minimal [65]. This contradicted the conclusion drawn by Jones and Hinesly, who suggested that K in shallow soil below a depth of 5 cm was easily washed away by water. Our findings indicate a relatively strong K-holding capacity of coastal forest soil, potentially serving as an adaptive strategy to a harsh environment of strong winds and high alkalinity (Na^+) [66,67].

4.2. Effects of Periodic Flooding on Soil C:N:P:K Stoichiometries

Soil C:N is commonly used as an indicator of soil N mineralization ability, which can partly reflect the accumulation of soil C and N through plant litter and root exudates [68]. In this study, flooding elevated the soil C:N ratio of the 0–10 cm layer. This was because the surface soil contained higher organic matter, whereas the quantity and activity of microorganisms were reduced by the flooding, resulting in a lower decomposition rate of soil organic matter and an elevated soil C:N [69]. Additionally, the soil C:N ratios of different layers in this study were lower than the average C:N ratio of terrestrial soil (11.9) in China, suggesting a stronger SOC mineralization in coastal forest soils [70]. After being flooded, soil C:P and N:P ratios of 0–10 and 20–30 cm layers both significantly decreased; this indicated that there were obvious N and P losses through leaching during the flooding process. Soil C:P ratio is a useful index of soil's capacity to absorb and fix phosphorus; it can also can be used to determine if soil organic matter is mineralized by microorganisms, potentially releasing phosphorus into or absorbing phosphorus from the environment [50]. The C:P ratios of all the soil layers in this study were lower than the average values of 61 terrestrial soils in China [71]. When soil has a lower C:P ratio, it becomes easier for microorganisms to decompose organic matter, releasing nutrients and increasing the available phosphorus content in soil [72].

Soil N:P can be used to evaluate N saturation status and nutrient limitation type. The soil N:P ratios of this study were lower than those of the terrestrial soil in China (3.9), as well as the average ratio of global scale (5.9) [70]. This suggested that the P fixation ability of coastal forest soil was relatively low. Additionally, the TN content ranged from 0.71 g/kg to 1.16 g/kg in this study, which was also lower than the TN content of terrestrial soil in China (2.30 g/kg), indicating that coastal forest soil was facing great N deficiency [73]. Besides, we observed a decreasing trend of C:K and N:K with the increasing soil depth, which was mainly due to the lower SOC and TN contents in deep soils [70]. Soil C:K and N:K ratios were also significantly lower than those of the normal soil after being flooded, resulting from the decreased C and N in flooded stands. Conversely, soil K content was minimally affected by the periodic flood and remained relatively stable.

4.3. Effects of Periodic Flooding on Correlations of Soil C, N, P, and K Stoichiometries

The correlation between soil C, N, P, and K stoichiometries showed various changes after being flooded. In normal soil, SOC exhibited significant positive correlations with TN and C:N, while flooding weakened the relationship, suggesting that flooding partially decoupled the C-N correlation [74]. Via PCA, it can be inferred that flooding diminishes SOC, leading to alterations in C:N ratios. After the flooding, there were no correlations observed between C:N and SOC or TN in the 0–10 and 10–20 cm layers, indicating that flooding stress resulted in the decoupling of soil C and N in surface and shallow soils [37,75]. In deeper soil layers (20–30 cm), the correlations between C, N, P, and K stoichiometries ratios became weaker than those of the surface soil in flooded stands, indicating that as soil depth increased, the coupling relationships of C, N, P, and K nutrients were reduced in strength. This was probably related to the slower rate of soil organic matter decomposition as well as the decreased litter input and microbial activity [76]. Overall, the correlations between C, N, P, K, and their stoichiometric ratios were relatively diverse in this study. This was attributed to the complexity of coastal shelterbelt habitats as well as the structure of soil biomes, and other biological and abiotic factors [77]. However, further study is still needed to investigate the specific C, N, P, and K cycling process in soil–plant systems and its underlying mechanisms after being flooded in coastal forests.

5. Conclusions

Periodic flooding altered the soil C, N, P, and K ecological stoichiometries in coastal shelterbelt forests of eastern China, but the differences were soil depth-dependent. Following flooding, there were notable variations in SOC and TN in each soil layer, but deeper soils were relatively less impacted. Flooding resulted in a reduction in SOC, TN, hydrolytic N and TP contents, while having minimal effect on TK content. The variations in soil C, N, P, and K stoichiometric ratios indicated that the SOC was susceptible to mineralization in the coastal forest and that the soils were N-deficient. Periodic flooding affected the relationships of soil C, N, P, and K nutrients and resulted in a clear decoupling trend between them, especially for the C-N correlation. The alterations in soil C, N, P, and K ecological stoichiometries and their correlations reflected the adjustment of soil ecological stoichiometry structure to periodic flooding, which may subsequently affect the plant growth rates in coastal shelterbelt forests. These results are expected to benefit the understanding of soil nutrient response to periodic flooding in coastal shelterbelt forests and provide a scientific basis for assessing the risk of soil nutrient loss and improving the soil quality in these frequently disturbed forests.

Author Contributions: B.B. and H.X. carried out the fieldwork and laboratory analysis, prepared the figures, and wrote the manuscript. M.C. and S.J. revised the manuscript; X.L. and H.X. contributed substantially to the study design and supervised the field and laboratory personnel. All authors have read and agreed to the published version of the manuscript.

Funding: The research was supported by the National Key Research & Development Project (2019YFE0118900) and the National Natural Science Foundation of China (32101506).

Data Availability Statement: Data are available on request from the authors.

Acknowledgments: We are grateful to Quanxin Zhang from the Forestry Bureau of Xiangshan County for his assistance in the fieldwork.

Conflicts of Interest: The views and conclusions in this document are those of the authors and should not be interpreted as representing the opinions or policies of the funding agencies and supporting institutions. The authors declare that they have no conflict of interest.

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