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Effects of Waterbird Herbivory on Dominant Perennial Herb *Carex thunbergii* in Shengjin Lake

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Abstract: Abundant food resources in riparian zones provide efficient foraging sites for waterbirds. Herbivory is a key ecosystem process that has widely recognized effects on primary production and vegetation structure and composition. However, there is limited understanding of impacts of waterbird herbivory on riparian zone vegetation. In this study, a bird enclosure experiment with five levels of foraging intensities (no foraging, very little foraging, light foraging, moderate foraging and heavy foraging) was set up in Shengjin Lake to study the effects of waterbird foraging on the community structure of sedge meadows and individual traits of the dominant plant *Carex thunbergii*. Foraging intensity had little effect on community structure. The dry mass of *C. thunbergii* decreased with the increasing foraging time. Waterbird foraging reduced leaf dry mass under heavy foraging by 27.7% and root dry mass by 45.6% compared to CK (no foraging). Waterbird foraging increased allocation to shoot growth but had a weak effect on elemental allocation of *C. thunbergii*. The foraging intensity significantly affected the morphological traits of *C. thunbergii*. The results of structural equation modeling showed that RSR (root: shoot ratio represents the ratio of dry mass) and RL (root length) are key traits in driving the dry mass decline in the presence of bird foraging. This study may contribute to a better understanding of the adaptability of perennial herb plants to waterbird foraging and maintain the healthy development of wetland ecosystems.

Keywords: bird foraging; *Carex thunbergii*; functional trait; community structure; riparian zone



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1. Introduction

As a part of wetland ecosystems, the riparian zone is the transition between aquatic and terrestrial ecosystems, playing significant roles in resisting floods, regulating climate and controlling water runoff [1,2]. During the dry season, lowering of water levels and surface cover will aggregate food resources in the riparian zone, which provides extremely efficient foraging sites [3]. The major factors that drive plant diversity and ecosystem function in wetlands are hydrology, nutrient availability and herbivores. However, there is limited understanding of the impacts of herbivores on riparian zone vegetation [4,5]. Most research of herbivory in wetlands has been conducted on insects, while other organisms, such as crayfish, fish and waterbirds, lead to a large decrease in plant biomass [6,7]. The lake wetlands in the middle and lower reaches of the Yangtze River are unique in the world, with many short-lived lakes, which are important stopover and wintering sites for migratory waterbirds on the East Asian-Australasian flyway [8]. It provides wintering grounds for more than 900,000 waterbirds, especially great amounts of herbivorous waterbirds [9]. Many studies have focused on the distribution of vegetation-influenced herbivorous waterbirds in the shallow lake riparian zone of the middle and lower reaches

of the Yangtze River [10]. However, the effect of waterbird foraging on plant vegetation is little known.

Herbivores can profoundly influence plant community structure and diversity in riparian zones [11–13]. The research of Veen showed that aquatic grazers, mostly waterbirds, reduced biomass of *Phragmites australis* and *Stratiotes aloides* by an average of 25% and 60%, respectively [14]. Herbivores in Shark Bay—which include dugongs, sea turtles and fishes—would selectively forage on high nutrient content, fast-growing tropical species when given a choice [15]. Some studies suggested that moderate grazing can maintain the productivity level and increase the species richness [16]. The dominant species with good palatability were preferred to be foraged under moderate grazing, thus providing more opportunities for slow-growing species [17]. Therefore, studying how waterbird foraging affects vegetation growth is helpful for us to understand the changes in plant community composition.

Plant functional traits are the features (morphological, physiological, or phenological) that represent ecological strategies and determine how plants respond to environmental factors, affect other trophic levels, and influence ecosystem properties [18]. Several studies have demonstrated that functional traits can reflect the contribution of plants to different ecosystems under grazing treatments [19,20]. While the riparian zone vegetation is mainly composed of clonal plants, few studies have considered how these root traits of dominant perennial herbs respond to herbivores [21]. Previous studies have mostly focused on leaf traits of plants [22,23]. However, root traits play important roles in nutrient absorption and transportation, and in ecosystem processes [24]. The dominant species in wetland plants are mostly clonal plants, and their underground (root system, rhizome, stolon, etc.) traits can determine plant fitness and better reflect plant responses to the external environment [25,26]. Our current study of *Carex thunbergii* in wetlands showed that roots play a crucial role in their growth. Therefore, when studying the functional traits of dominant plants in wetlands, more consideration should be given to the changing of related underground functional traits.

The Shengjin Lake is an important wintering place and stopover site for migratory waterbirds on the East Asian-Australasian flyway [27]. Waterbirds generally arrive in late October and fly away in early April. The species and number of overwintering waterbirds reached the maximum from December to January of the following year. Seasonal fluctuations in water level have formed a large riparian zone in Shengjin Lake, providing many food resources and habitats for waterbirds. *C. thunbergii* is a common and dominant species in the riparian zone of Shengjin Lake and is a dominant food type for the wintering geese, mainly composed of bean geese (*Anser fabalis*) and greater white-fronted geese (*A. albifrons*) [27,28]. This study analyzes the effects of bird foraging on the community structure of sedge meadows and individual traits of the dominant plant *C. thunbergii* by a bird enclosure experiment. In this context, we addressed the following questions: (1) What is the effect of different foraging intensities on plant community composition? (2) What are the effects of different foraging intensities on functional traits? (3) How do foraging intensities affect dry mass changes?

2. Materials and Methods

2.1. Study Site

This study area was located at the Shengjin Lake (30°15' N–30°30' N, 116°55' E–117°15' E) (Figure 1), a shallow lake connected to the Yangtze River on the East Asian-Australasian flyway. The region belongs to a humid subtropical monsoon climate, with an average annual temperature of 16.4 °C and annual precipitation of 1600 mm. There is a clear separation between the rainy and dry seasons. The rainy season is from April to October, and the dry season lasts from November to March in the following year [29]. In the dry season, large areas of mudflats and exposed sedge (*Carex* spp.) meadows supply foraging habitats for the migratory waterbirds. Dominant plants in the lake are the *Carex* and *C. thunbergii*, accounting for 80–90% of the vegetation cover of the total plant community.

The periodical change of hydrology in Shengjin Lake makes the riparian zone have a seasonal plant growth cycle. The *Carex* community has two growing seasons per year, the first from October to November. When the temperature started to rise in mid-February, the *Carex* began to grow again on the fluctuating zones [30]. Shengjin Lake provides abundant food resources to attract waterbirds for foraging and become important habitats for waterbirds.

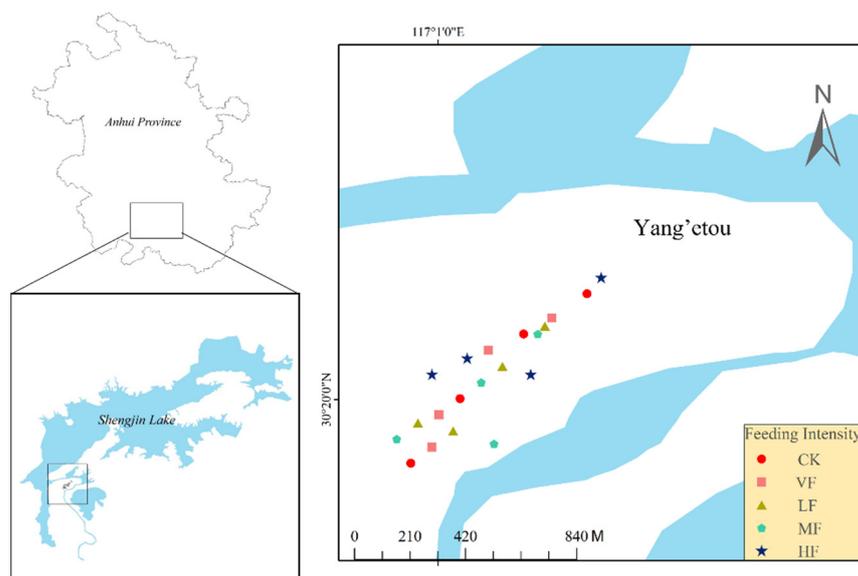


Figure 1. The location of the study area. Different colors represent different foraging intensity (CK, no foraging; VF, very little foraging; LF, light foraging; MF, moderate foraging; HF, heavy foraging).

2.2. Experimental Design

To test for waterfowl effects, a bird exclusion experiment with 5 treatments and 4 replicates, making a total of 20 plots, was established in October 2020 [31]. Sixteen exclusion plots consisted of stone pillars and nets (mesh size: 5 cm × 5 cm) to keep waterfowl from getting in and protecting the vegetation. There were 4 bird accessible plots only with stone pillars but without a net. The treatments were 5 levels of different exclusion time: (CK, no foraging; exclusion from 19 November 2020 to 24 March 2021; VF, very little foraging; exclusion from 19 November 2020 to 21 February 2021; LF, light foraging; exclusion from 19 November 2020 to 19 January 2021; MF, moderate foraging; exclusion from 19 November 2020 to 19 December 2020; HF, heavy foraging; no exclusion) (Table 1). We harvested the leaves and roots of *C. thunbergii* on 24 March 2021.

Table 1. The parameters of foraging intensity and the measurement index.

Terms	Explanation	Terms	Explanation
CK	no foraging	SLA	specific leaf area
VF	very little foraging	RL	root length
LF	light foraging	RD	root diameter
MF	moderate foraging	RSA	root surface area
HF	heavy foraging	RV	root volume
C	carbon	NL	number of links
N	nitrogen	NT	number of tips
P	phosphorus	RSR	root: shoot ratio
LC	leaf carbon	RC	root carbon
LN	leaf nitrogen	RN	root nitrogen
LP	leaf phosphorus	RP	root phosphorus

2.3. Community Structure

In each plot, 1 m × 1 m quadrat was randomly laid down. In each quadrat, plant species were identified and the number of individuals of each species were counted. To assess differences in species diversity under different foraging intensities, we measured species richness, the Shannon–Wiener diversity index and the Simpson index in March 2021 [32].

2.4. Morphological Trait of *C. thunbergii*

In each 1 m × 1 m quadrat, a random 25 cm × 25 cm sub-quadrat was dug out carefully. The plants were carefully uprooted, roots were thoroughly washed three times to remove impurities, and samples were then stored at −4 °C and brought to the laboratory. Five *C. thunbergii* plants were randomly selected and labeled in each plot for height measurement and subsequent analysis. All the plants were then separated into different tissues of leaves and roots, and they were oven-dried at 65 °C for 48 h and weighed [33]. We randomly selected five plants to measure leaf area with a leaf area meter (Li-3000, Li-COR). The specific leaf area (SLA) was calculated as the leaf area/leaf dry mass [34]. Meantime, each root from the same individuals was spread out on paper to reduce root overlap and scanned using a flatbed scanner (EPSON Perfection V700 Photo, Seiko Epson Corp., Suwa, Japan) at a resolution of 400 dpi. Root measurements were conducted using Win-RHIZO image analysis software (Regent Instruments Inc., Quebec, QC, Canada). Root traits including root length (RL), root diameter (RD), root surface area (RSA), root volume (RV), number of links (NL) and number of tips (NT) were calculated.

2.5. Chemical Traits of *C. thunbergii*

The samples of leaf and root were ground and homogenized with a mill (MM400, Retsch, Germany). The leaf and root carbon (C), and nitrogen (N) were determined using an elemental analyzer (vario MICRO cube; Elemental, Germany). After digestion in a mixture of H₂SO₄ and H₂O₂, a TU-1901DS ultraviolet spectrophotometer UV-2300 (Tecomp Com, Shanghai, China) molybdenum antimony colorimetric method was used to quantify leaf and root phosphorus (P) [35].

2.6. Data Analysis

Statistical analyses were performed with version 26.0 of the SPSS software (SPSS Inc., Chicago, IL, USA). We used one-way analysis of variance (ANOVA) to test the differences in community composition, biomass of *C. thunbergii*, morphological traits, and chemical traits among the different foraging intensities. When the ANOVA results were significant, we performed the least significant difference (LSD) test to identify differences between foraging treatments. Differences were considered statistically significant when $p < 0.05$. The principal components analysis (PCA) was conducted on the traits of *C. thunbergii* to analyze the relationships between the functional traits and the foraging intensities. PCA were performed with version 4.0.5 of R (R Core Team, 2021) [36]. Structural equation modeling (SEM) was also employed to explore how foraging intensities affected *C. thunbergii* dry mass through traits. The analysis was performed with AMOS (AMOS, v18, IBM, Chicago, IL, USA) and the best model based on multiple indicators were chosen with standardized correlation coefficients, including chi-square (χ^2), p , comparative fit index (CFI), root mean square error of approximation (RMSEA) [37]. We produced the figures using version 8.0 of the Origin Pro software (Origin lab Corporation., Northampton, MA, USA).

3. Results

3.1. Plant Community Diversity

There were no significant differences in richness, Simpson index and Shannon–Wiener diversity index between CK, MF and HF (Figure 2A–C). The species richness under VF was 3 and under LF was 5 (Figure 2A). The Shannon–Wiener diversity index of treatment

VF was lower than in LF by 55.8%, whereas the Simpson index of treatment VF compared with LF decreased by 57.4%.

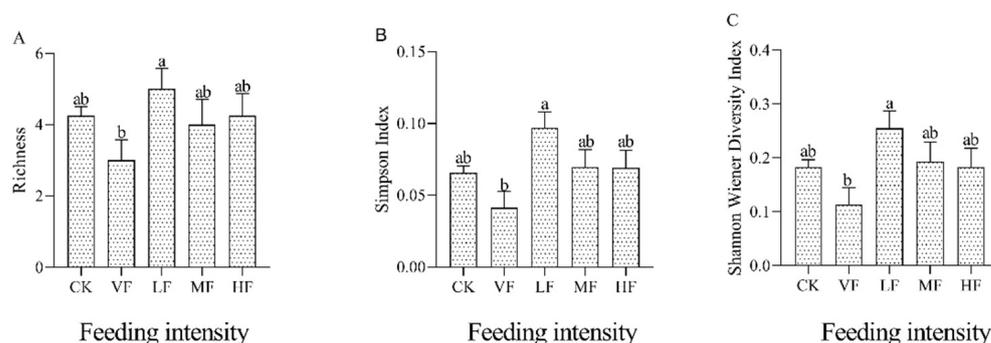


Figure 2. Diversity of plant communities in different foraging intensities (CK, no foraging; VF, very little foraging; LF, light foraging; MF, moderate foraging; HF, heavy foraging) showing (A) richness, (B) Simpson index, (C) Shannon–Wiener diversity index. In each graph, means with the same lowercase letters are not significantly different among foraging intensity ($p > 0.05$); means with different lowercase letters are significantly different among foraging intensity ($p < 0.05$). Capped lines represent \pm standard error.

3.2. Biomass of *C. thunbergii*

The root fresh weight decreased with the increase of foraging intensity (Figure 3A). Root fresh weight was the highest under CK and the lowest under HF, which was 260.5. There was no significant difference in leaf fresh weight ($p > 0.05$). Root dry weight also decreased with the increase of foraging intensity (Figure 3B). Root dry weight was significantly higher than leaf dry weight. Leaf dry weight under HF was reduced by 27.7% compared to CK, while root dry weight was reduced by 45.6% compared to CK ($p < 0.05$). As the foraging intensity increased, the root: shoot ratio showed a downward trend (Figure 3C), and under LF, MF, HF, it was significantly lower than CK ($p < 0.05$).

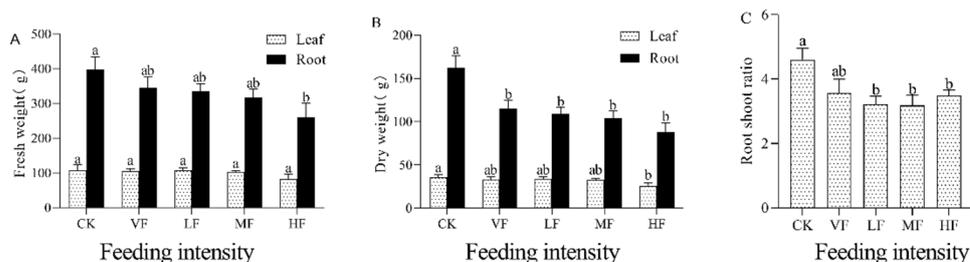


Figure 3. Biomass of *C. thunbergii* in different foraging intensities (CK, no foraging; VF, very little foraging; LF, light foraging; MF, moderate foraging; HF, heavy foraging) showing (A) fresh weight, (B) dry weight, (C) root: shoot ratio. In each graph, means with the same lowercase letters are not significantly different among foraging intensity ($p > 0.05$); means with different lowercase letters are significantly different among foraging intensity ($p < 0.05$). Capped lines represent \pm standard error.

3.3. Plant Morphological Traits

The foraging treatment had a significant effect on plant height (Figure 4A, $p < 0.05$). The plant height was highest in CK, with a height of 89 cm, and was lowest in HF, with a height of 71 cm. The differences in plant height of SF, LF and MF were not significant, and were all higher than HF. SLA significantly decreased with increasing foraging intensity. SLA under MF was 76.8 (Figure 4B). There was no significant difference in leaf area (LA) among the treatments (Figure 4C, $p > 0.05$). Five root traits—RL, RSA, RV, NT, NL—were strongly inhibited by foraging and declined with increased foraging intensity (Figure 4D–I). RL under HF was 60% lower than CK.

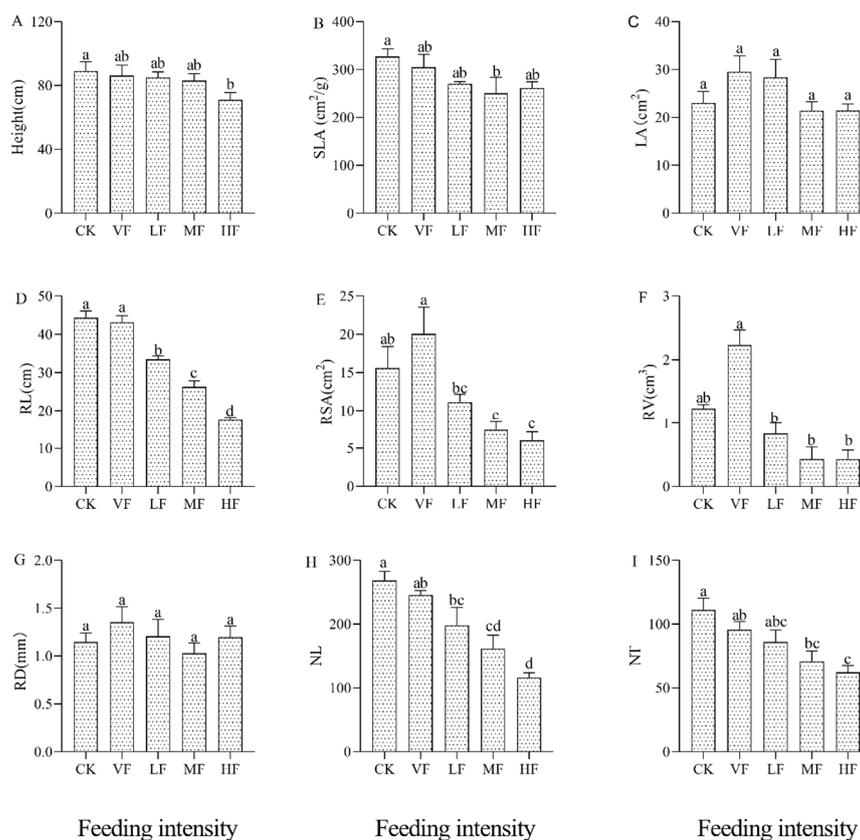


Figure 4. Morphological trait of *C. thunbergii* in different foraging intensity (CK, no foraging; VF, very little foraging; LF, light foraging; MF, moderate foraging; HF, heavy foraging) showing (A) plant height; (B) specific leaf area, SLA; (C) leaf area, LA; (D) root length, RL; (E) root surface area, RSA; (F) root volume, RV; (G) root diameter, RD; (H) numbers of links, RL; (I) numbers of tips, NT. In each graph, means with the same lowercase letters are not significantly different among foraging intensity ($p > 0.05$); means with different lowercase letters are significantly different among foraging intensity ($p < 0.05$). Capped lines represent \pm standard error.

3.4. Chemical Traits

There was no significant difference in leaf C, N and P (Table 2). Leaf N and P were significantly higher than that of the roots. The leaf N under HF was higher than CK. The root N was 0.8 under HF, which was lower than CK. The leaf P was highest under CK and was lowest under MF.

Table 2. C, N and P concentrations of leaf and root of *C. thunbergii* in different foraging intensity.

Parameters		Foraging Intensity				
		CK	VF	LF	MF	HF
C (%)	Leaf	43.35 \pm 1.06 ^a	44.38 \pm 0.64 ^a	42.69 \pm 1.22 ^a	42.97 \pm 0.98 ^a	41.95 \pm 1.39 ^a
	Root	45.86 \pm 0.64 ^a	43.80 \pm 1.01 ^{ab}	41.70 \pm 0.79 ^b	45.21 \pm 0.83 ^a	44.35 \pm 1.01 ^{ab}
N (%)	Leaf	2.14 \pm 0.11 ^a	2.20 \pm 0.18 ^a	2.18 \pm 0.25 ^a	2.16 \pm 0.13 ^a	2.23 \pm 0.15 ^a
	Root	0.97 \pm 0.04 ^{abc}	1.06 \pm 0.05 ^{ab}	0.93 \pm 0.07 ^{bc}	1.12 \pm 0.03 ^a	0.81 \pm 0.04 ^c
P (%)	Leaf	0.27 \pm 0.06 ^a	0.22 \pm 0.04 ^a	0.20 \pm 0.03 ^a	0.19 \pm 0.03 ^a	0.22 \pm 0.06 ^a
	Root	0.13 \pm 0.01 ^{ab}	0.12 \pm 0.03 ^b	0.18 \pm 0.01 ^a	0.12 \pm 0.01 ^b	0.13 \pm 0.02 ^{ab}

^{a,b,c} rows with different superscript are significantly different ($p < 0.05$) for each treatments. The values are mean \pm standard errors. (CK, no foraging; VF, very little foraging; LF, light foraging; MF, moderate foraging; HF, heavy foraging; H, plant height; C, carbon; N, nitrogen; P, phosphorus).

3.5. PCA Analysis

As shown in Figure 5, the first two principal components of the PCA for the functional traits of *C. thunbergii* explained 51.7% of the variation under the different foraging intensities. The first principal component explained 35.7% of the variation and was positively correlated with height (H), RV, RSA, RL and NT (Figure S1). The second principal component explained 16% of the variation and was positively correlated with LN, RP and LP. The difference between CK and VF is not obvious, and CK can be clearly distinguished from MF and HF.

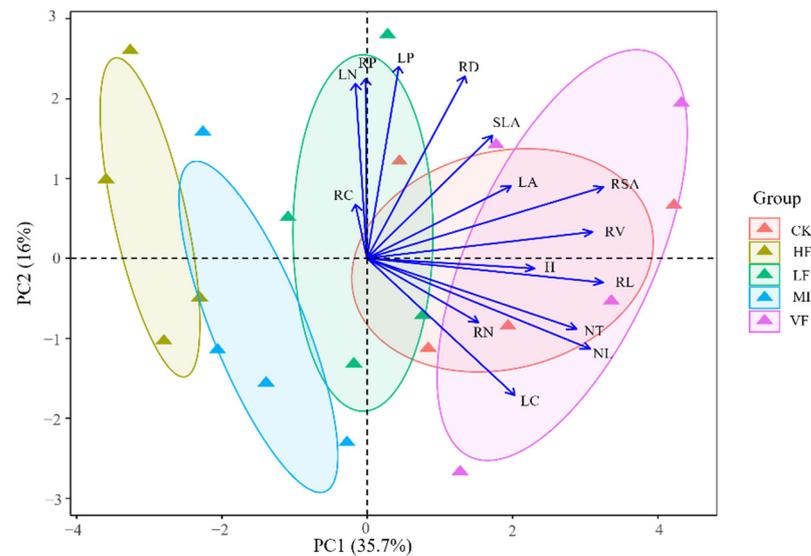


Figure 5. Principal components analysis (PCA) of *C. thunbergii* traits. (CK, no foraging; VF, very little foraging; LF, light foraging; MF, moderate foraging; HF, heavy foraging; H, plant height; SLA, specific leaf area; LA, leaf area; RL, root length; RSV, root surface area; RV, root volume; RD, root diameter; NT, numbers of tips; NL, numbers of links; LC, leaf carbon; LN, leaf nitrogen; LP, leaf phosphorus; RC, root carbon; RN, root nitrogen; RP, root phosphorus.).

3.6. Pathways That Directly or Indirectly Affect Dry Mass

SEM indicated that 99% of the variation in root dry mass was explained by H, SLA, RSR, RL, NL and leaf dry mass, with significantly correlated pathways from RSR ($r = 0.87$, $p < 0.001$) and leaf dry mass ($r = 0.81$, $p < 0.001$) (Figure 6). There were also positively correlated pathways from NL to height, and RL to NL. Foraging intensity mainly affected height, SLA, RSR and RL in negative ways, and was significant with SLA, RSR and RL.

The SEM was created to quantify the direct and indirect effects of bird foraging and plant traits on the dry mass of *C. thunbergii*. Bird foraging had a direct negative effect on leaf dry mass and had a positive effect on root dry mass. In addition, bird foraging indirectly reduced leaf dry mass through RL. Bird foraging indirectly affected root dry mass through RL and RSR.

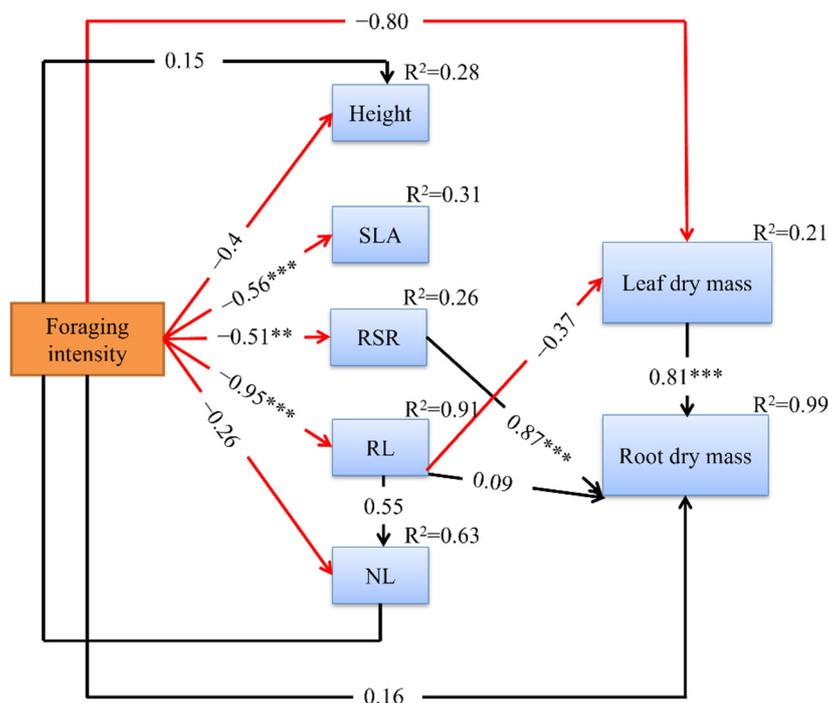


Figure 6. Structural equation modeling (SEM) of foraging intensity as a predictor of leaf dry mass and root dry mass through direct and indirect effects mediated by changes in height, SLA, RSR, RL, and NL. Models show the direct and indirect effects of how bird foraging and plant traits on dry mass of *C. thunbergii*. (chi-square (χ^2) = 15.245, degree of freedom (df) = 13, p = 0.292, comparative fit index (CFI) = 0.987, root mean square error of approximation (RMSEA) = 0.095). Red and black solid arrows represent negative and positive pathways, respectively. Numbers are the standardized path correlation coefficients (Pearson's r). R^2 denotes the proportion of variance explained by indicators of the model. Significance at 95% confidence level: ** p < 0.01; *** p < 0.001.

4. Discussion

Our results showed that bird foraging was closely related to the changes in the root traits of *C. thunbergii*. The height, SLA and root traits were the highest under CK, and decreased with the increase of foraging intensity. However, we found that foraging intensity had no significant effect on the C, N and P. Under heavy foraging, leaf dry mass was reduced by 27.7% and root dry mass was reduced by 45.6% compared to CK. The dry mass of *C. thunbergii* was influenced indirectly by RL and RSR. In future studies on perennial herbs in riparian zones, we should pay more attention to root traits as they provide unique information about how a plant is adapted to bird foraging.

4.1. Effect of Different Foraging Intensity on the Diversity of *Carex* Community

The vegetations are mostly *Carex* communities in sedge meadow, which are important food stocks of wintering herbivorous geese in the middle and lower Yangtze River floodplains, in particular *A. fabalis* and *A. albifrons* [38]. Herbivorous birds could lead to the large reduction in plant standing crops, especially for the birds that are non-breeding and gregarious [39]. In addition, the selective foraging pressure of herbivorous birds is a key factor driving the changes of vegetation structure and species diversity [15]. Our enclosure experiment showed that the moderate foraging increased the alpha diversity index of the *Carex* community, and all three diversity indices were the highest under LF. This is consistent with the previous research and is in line with the hypothesis of moderate interference in the community [17]. Therefore, the higher species diversity observed under LF may be related to fewer herbivore foraging choices [40]. Our results are inconsistent with the study of Xiang, probably due to Shengjin Lake having a high level of productivity [41]. Compared

with LF, VF showed a decrease in plant diversity which may indicate that waterbirds began to forage green, newly grown plants, instead of foraging *C. thunbergii*. Some studies showed that grazing waterbirds, such as geese, often selected plants offering the highest nitrogen intake [42], and nitrogen content generally decreases with increasing plant height [43]. In addition, vegetation of intermediate height provides waterbirds with perches and shelter, whereas extremely high vegetation interferes with foraging [44]. Under VF treatment, waterbirds have entered the late migration stage, and *A. albifrons* have to replenish a lot of energy for the return migration. At this time, *C. thunbergii* entered a period of rapid growth, and the protein content drops, making the grass unpalatable. White-fronted geese are selective foragers and they usually choose specific plant species to forage based on the nutritional value of plant. Accordingly, waterbirds began to forage some companion species, leading to a decrease in diversity under VF. Thus, more attention should be paid to the selective foraging of herbivorous goose and consequent impacts on vegetation and ecosystem function.

4.2. Dry Mass and Elemental Allocation of *C. thunbergii* under Different Foraging Intensity

Considering the greater premium on plant quality and limited ability to digest cellulose and other highly recalcitrant plant parts, herbivorous bird species mostly foraged on the fast-growing and energy-rich food items, these foods being mainly dominant plants [45,46]. Several reports have shown that *Carex* spp. dominate the diet of herbivorous geese in various shallow lakes of the middle and lower Yangtze River floodplain [47]. Consistent with the literature, this research found that the dry mass of *C. thunbergii* showed a downward trend with increasing foraging time (Figure 3). Leaf dry mass under HF was reduced by 27.7% compared to CK. The root dry mass was reduced by 45.6% compared to CK. The root dry mass decreased more than the leaf, probably because the leaves resumed growth after birds' migration. We harvested the plants on 24 March 2021. Wintering waterbirds depart in March. Rising temperature and the migration of waterbirds have led to a recovery of growth of *C. thunbergii* [48]; the leaves begin to grow and the roots continue to accumulate. In addition, wetlands have high levels of productivity [49]. From the results of the diversity, it can be found that birds foraging is not heavy, so leaf dry mass changes are not very large. The root: shoot ratio reflects the proportion of photosynthates that are allocated to the leaf and root [50]. The root dry mass of *C. thunbergii* was higher than the leaf dry mass under different foraging intensities. This is because some wetland plants, such as *C. cinerascens* have the characteristic of distributing more biomass to the root system to adapt to the flooded environment [51]. As the foraging time increased, the root: shoot ratio of *C. thunbergii* decreased significantly. Some literature suggests that increased allocation to shoots following grazing may represent an evolutionarily adaptive trait for grazing tolerance [52]. This finding is contrary to previous studies and may be due to the fewer foraged leaves at the end of migration as waterbird numbers decline [53]. Herbivory has often been reported as contributing to enhanced tissue nutrient (N and P) concentrations in plants [54]. Our results showed that the leaf C, N and P concentrations of *C. thunbergii* (Table 2) was not significantly affected by bird foraging. The N and P concentration of *C. thunbergii* roots followed a unimodal curve with the increase of foraging intensity. Overall, herbivory has a weak effect on the elemental allocation of *C. thunbergii*. The nutrient content of the dominant species did not change significantly, indicating that the dominant species had stress resistance and could self-balance [55]. A global meta-analysis also suggested that the effect of increasing plant N and P concentration under herbivory is much weaker at the species level compared to the community level and the major mechanism driving the plant community level stoichiometric responses to herbivory was the change of vegetation structure [56].

4.3. Functional Traits of *C. thunbergii* under Different Foraging Intensity

Plant functional traits which link to ecosystem functions are basic elements that adapt to grazing [57]. As the main plant organ that is consumed by herbivores, leaves are strongly

affected by grazing and are an important indicator organ for changes of plant growth [58]. In this study, we observed that all the leaf traits tested in this study, including plant height and SLA, decreased with increasing foraging time (Figure 4). Similarly, the deer enclosure experiment conducted by Herbering et al. also suggested that *Maianthemum racemosum* had decreased SLA by 33% in deer access areas as compared to exclusion areas [59]. Our results are inconsistent with the study of Wang, which may be because *C. thunbergii* mainly adopts protection strategies when being eaten [20]. That is, lower SLA means thicker cell walls and leaves that can increase the protection against herbivores [28]. Root traits are closely related to nutrient absorption and plant adaptation strategies to biotic and abiotic stress [60]. In our study, *C. thunbergii* roots tended towards miniaturization in response to bird foraging. Five root traits (RL, RSA, RV, NL and NT) decreased substantially when plants were subjected to bird foraging. Root miniaturization inhibits the ability of roots to acquire nutrients and water, which may explain the reduction in plant size and SLA [50]. Root miniaturization of *C. thunbergii* will allow companion species to occupy more underground space, which may also be a reason for changes in community diversity [61].

4.4. Mechanism of Bird's Foraging-Induced Biomass Decrease

By analyzing a set of functional traits, we could distinguish the *C. thunbergii* with heavy foraging from those of other treatments in a PCA (Figure 5). The first principal component obtained by PCA was mainly related to shape and size of plants (e.g., height, root volume, root surface area, root length, and numbers of tips). The PC1 distinctly separated HF with lower height, root length and surface area from CK. However, CK and SF cannot be separated clearly by the PCA analysis. The second principal component was mainly related to plant elemental allocation (leaf N concentration, leaf P concentration and root P concentration), represented by strong positive co-variation between LP and RP. It suggested that the change of P concentration in *C. thunbergii* was independent of bird foraging. Direct and indirect paths of *C. thunbergii* dry mass decline induced by bird foraging were fitted using SEM (Figure 6). Bird foraging experiments showed that 99% root dry mass of *C. thunbergii* were explained by height, SLA, RSR, RL, NL and leaf dry mass, and bird foraging indirectly affected root dry mass through RL and RSR. Our results highlight that RSR and RL are key traits in driving the dry mass decline in the presence of bird foraging. These are inconsistent with the study of Zhao, which may due to root traits being important adaptive characteristics of wetland plants [51,62]. Our results highlight that root length plays an important role in dry mass decline than leaf traits. Considering the above results, it will be necessary, in future studies on perennial herbs in riparian zones, to place more consideration on root trait variation pattern as it provides unique information about how a plant is adapted to bird foraging.

5. Conclusions

Our results showed that the foraging intensity significantly affected the morphological traits of *C. thunbergii*. Waterbird foraging increased allocation to shoot growth but had a weak effect on elemental allocation of *C. thunbergii*. Under heavy foraging, root dry mass decreased more than leaf dry mass. The results of structural equation modeling showed that RSR and RL are key traits in driving the dry mass decline in the presence of bird foraging. This study may contribute to a better understanding of the impacts of waterbird foraging on vegetation and ecosystem function.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d14050331/s1>, Figure S1: Quality of representation of *Carex thunbergii*. The larger the value, the greater the contribution of the variable to the principal components analysis (PCA) result. H, plant height; SLA, specific leaf area; LA, leaf area; RL, root length; RSV, root surface area; RV, root volume; RD, root diameter; NT, numbers of tips; NL, numbers of links; LC, leaf carbon concentration; LN, leaf nitrogen concentration; LP, leaf phosphorus concentration; RC, root carbon concentration; RN, root nitrogen concentration; RP, root phosphorus concentration.

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