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Effects of flooding duration on wetland plant biomass: The importance of soil nutrients and season

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Abstract

1. Extensive studies have shown that the relationship between flooding duration and wetland plant biomass is context specific. The underlying mechanisms, however, are uncertain. A likely explanation is that flooding has both direct effects by exerting stress on plants and indirect effects by affecting soil nutrient availability. The net effect would be context-specific and might depend on season. Here, we tested two potential factors mediating the flooding effects on wetland plant biomass: soil nutrient availability and season.
2. We carried out a field investigation in the lakeshore meadows of the Poyang Lake floodplain, China, along a flooding duration gradient during the non-flooding period. To test the interaction between flooding duration and soil nutrients, we carried out a nutrient (N and P) addition experiment in two types of communities with different flooding durations.
3. The above-ground biomass (AGB) decreased with flooding duration in winter but had a quadratic response in spring, suggesting that the direct negative effect of flooding was stronger in winter than in spring. Soil total N content, total P content, and N:P ratio showed quadratic responses to flooding duration.
4. Our results supported the hypotheses that the influence of nutrient limitation decreased with flooding duration and was greater in spring than in winter. The evidence showed that, with longer flooding duration and in winter than in spring, the correlations between AGB and soil nutrient content were weaker, leaf N and P content of *Carex cinerascens* were stronger, and AGB response ratio to nutrient addition was lower. Meanwhile, the relative importance of N versus P to wetland plant biomass varied with flooding duration.
5. Consequently, indirect effects of flooding duration on AGB via soil nutrient availability were much less important than direct effects in winter or with long flooding duration, but were more important in spring or with short flooding duration. Therefore, the effects of flooding on wetland plant biomass depended on flooding duration, soil nutrient availability, and season.

KEYWORDS

above-ground biomass, flooding stress, nutrient addition experiment, nutrient limitation, zonation

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1 | INTRODUCTION

Flooding is an essential factor in controlling biodiversity and ecosystem functioning in wetland ecosystems (Keddy, 2010). Global climate change is changing the flood risk in many areas, altering the flooding regimes of wetland ecosystems (Hirabayashi et al., 2013). Furthermore, the flooding regimes of more than half of the world's major rivers have been changed by >50,000 large dams (Goodwin et al., 2014; Munoz et al., 2018). Many studies have documented that changes in flooding regimes could significantly affect wetland plant growth, but the effects varied (Garssen et al., 2015; Greet et al., 2011). Wetland plants provide various ecosystem services (Mitsch et al., 2015), such as sediment trapping, providing carbon for aquatic food webs and habitat for birds and fishes. Therefore, it is important to understand the mechanism of flooding duration effects on wetland plant growth under climate change and human activities.

Results concerning flooding duration effects on wetland plant biomass are inconsistent (Garssen et al., 2017; Wang, Chen, et al., 2014; Wang, Han, et al., 2014). Given that plant species have diverse phenologies and seasonal growth patterns, one potential explanation is that the sampling season differed among these studies (Wang et al., 2016). For example, Garssen et al. (2017) found that plant biomass was positively correlated with flooding duration in summer, while Wang, Chen, et al. (2014) and Wang, Han, et al. (2014) found a negative correlation in spring. However, it is unclear how flooding stress changes with season during the non-flooding period. We hypothesised that flooding stress would decrease as the non-flooding period extended (hypothesis 1), because wetland plants recovered during the non-flooding period and narrowed the gap with results in the control treatment (Chen & Xie, 2009),

Another potential explanation is that multiple mechanisms underlie the effects of flooding duration on wetland plant biomass. Flooding duration could have direct and indirect effects on plant growth (Keddy, 2010; Lan, Chen, et al., 2019; Figure 1a). Flooding duration could affect soil nutrient availability (Shrestha et al., 2014; Wright et al., 2015), which is important to wetland plants (Keddy, 2010), and thus indirectly affects wetland plant growth (Garssen et al., 2017). Flooding could affect the processes of sedimentation (Keizer et al., 2018; Noe et al., 2019), soil erosion (Carmignani & Roy, 2017), litter decomposition (Bai et al., 2005), and chemical reactions relating to nutrient leaching to water (Baldwin & Mitchell, 2000; Sollie et al., 2008). The overall effects of flooding on soil nutrient availability could be site-dependent, because these processes varied among different study sites. Although many studies have tested direct effects of flooding duration on plant growth (Garssen et al., 2015), only a few studies have explored indirect effects and relative importance of each pathway (Lan, Chen, et al., 2019).

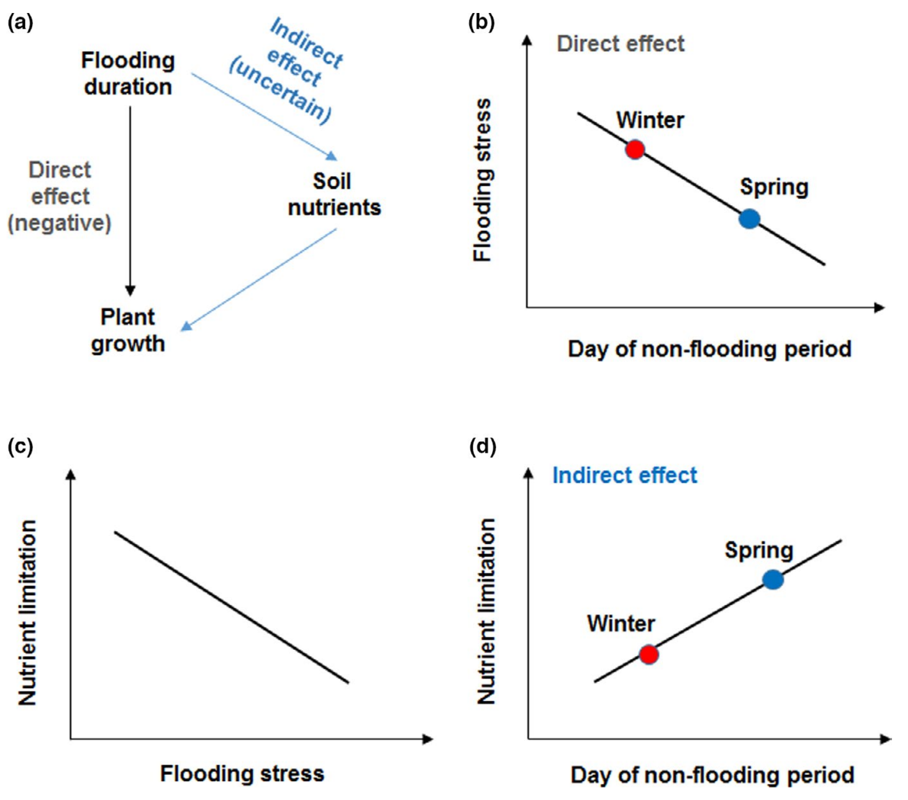

FIGURE 1 (a) Conceptual model showing the direct and indirect effects of flooding duration on plant growth. (b) Hypothesis about the relationship between days of non-flooding period and the importance of flooding stress; prediction that the importance of flooding stress would be smaller in spring than in winter. (c) Hypothesis about the trade-off between nutrient limitation and flooding stress. (d) Prediction that nutrient limitation would decrease with days of non-flooding period and be greater in spring than in winter

The effects of enhanced soil nutrient on wetland ecosystems varied among different studies (Ket et al., 2011; Traut, 2005), and the mechanism was unclear. Nutrient limitation of plant growth depends not only on soil nutrient availability, but also on many other factors (Ostertag & Dimanno, 2016). According to the stress gradient hypothesis, resource competition usually decreases with environmental stress intensity (He et al., 2013). In a previous study, with decreasing flooding stress along the flooding duration gradient, the importance of nutrient limitation increased (Lan, Chen, et al., 2019). We hypothesised that there would be a trade-off between flooding stress and nutrient limitation (hypothesis 2; Figure 1c). Plant growth with longest flooding duration could thus be limited by flood stress, whereas plant growth with shortest flooding duration could be limited by soil nutrient availability, which could result in maximum productivity in the middle of the gradient.

In this study, we aimed to address two questions: (1) How do flooding duration, season, and their interaction affect wetland plant productivity during the non-flooding period? (2) How do direct and indirect effects of flooding duration on wetland plant biomass change with season? To answer these questions, we carried out a field investigation along a flooding duration gradient (*c*. 130–350 days) in the lakeshore meadows of the Poyang Lake floodplain, China. To test the effects of soil nutrient availability on wetland plant biomass, we carried out a nutrient (N and P) addition experiment in two types of communities with different flooding durations.

According to hypothesis 1, we predicted that the direct effects of flooding stress would be greater in winter than in spring (Figure 1b), because winter is the early stage of the non-flooding period, and spring is the late stage in Poyang Lake. With greater flooding stress, the relationship between flooding duration and plant biomass would be stronger. According to hypotheses 1 and 2, we predicted that nutrient limitation would be greater in spring than in winter (Figure 1d). We adopted three indices of nutrient limitation: the relationship between soil nutrient availability and biomass, leaf nutrient content, and response of biomass to nutrient addition. With greater nutrient limitation, the relationship between soil nutrient availability (i.e. soil nutrient content) and above-ground biomass (AGB) would be greater, leaf nutrient content would be lower, while the response of AGB to nutrient addition would be greater.

2 | METHODS

2.1 | Study site

This study was carried out in Dahuchi Lake and neighbouring Chizhou Lake (Figure 2a), which are located at Poyang Lake National Reserve (28°22′N–29°45′N; 115°47′E–116°45′E), Jiangxi Province, China. These two lakes are located at the river mouth of Ganjiang River and Xiuhe River to the main lake of Poyang Lake. These two lakes are

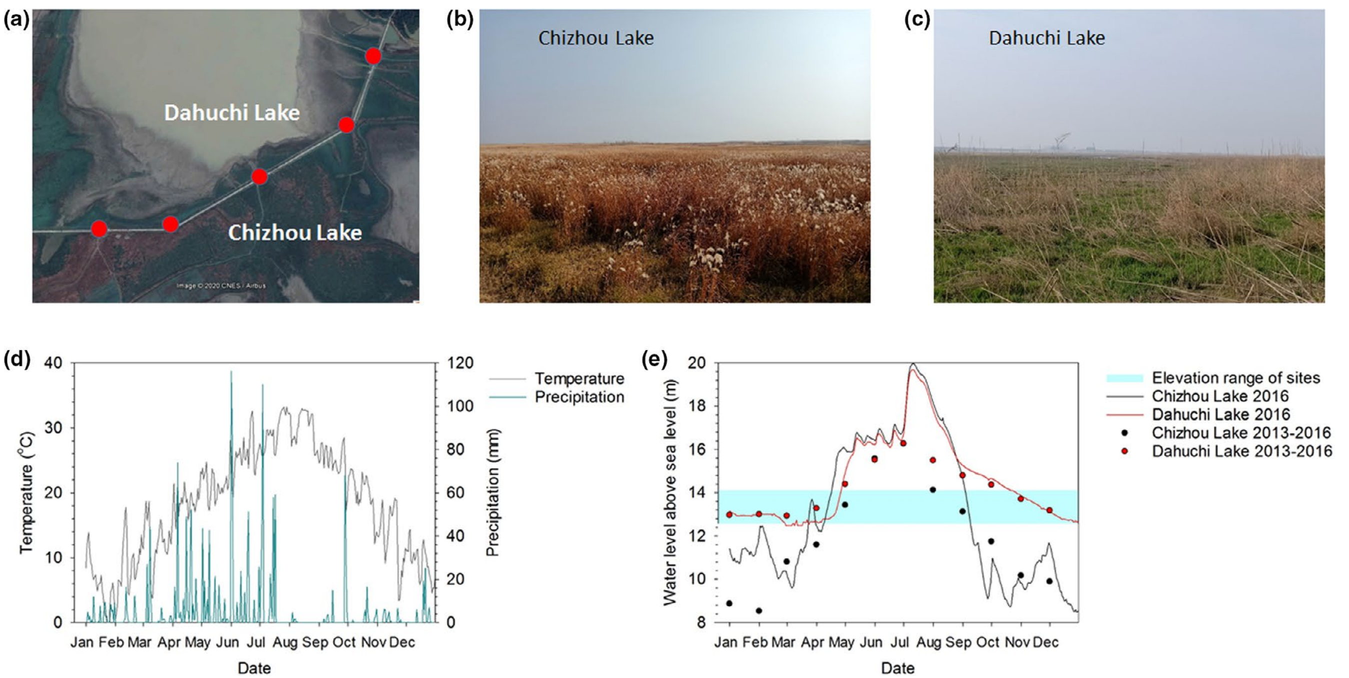

FIGURE 2 (a) A map taken from Google Earth, showing the vegetation of the Dahuchi Lake and the Chizhou Lake on 10 December 2017. Red circles indicate the locations of five sampling blocks. (b) Picture of vegetation from Chizhou Lake on 15 December 2019, with the dominant species *T. lutarioriparia*. (c) Picture of vegetation from Dahuchi Lake on 15 December 2019, with the dominant species *C. cinerascens*. (d) Daily temperature and temperature of 2016 in the study area. (e) Water levels of Chizhou Lake and Dahuchi Lake. Elevation ranges of sampling sites were similar between the two lakes. For clarity, we merged the elevation ranges of these two lakes in the figure

usually impounded by these two rivers and connected with the main lake of Poyang lake during the flooding period. Mean annual temperature is 17.1°C. The mean annual precipitation is 1,426.4 mm, and precipitation mainly occurs from April to June (Figure 2d). In the river mouths of Ganjiang River and Xiuhe River, mean total N concentration of lake water was 1.89 mg/L, and mean total P concentration was 0.087 mg/L (Liang et al., 2015). Mean total soil organic C content in the river mouths was 29.5 g/kg, total N content was 2.11 g/kg, total P content was 0.71 g/kg, available N concentration was 135.8 mg/kg, and available P concentration was 22.4 mg/kg (Wang et al., 2016).

During the non-flooding period, these two lakes are separated by a 2.6-m high levee built in 2013, and during the flooding period, the lakes are connected by flowing water (Figure 2a). The water level of Dahuchi Lake is controlled to prolong the flooding duration, while the water level of Chizhou Lake mainly follows a natural flooding regime (Figure 2e). During the flooding period (May–September), all floodplain meadows are submerged, while during the non-flooding period (October–April), most meadows emerge above the water level, and wetland plant species sprout and grow (Figure 2e). Therefore, peak wetland plant biomass occurs in mid-April (spring) and early December (winter), and most of the plants die in January. Along the elevation gradient of the lakeshore, zonation patterns of plant communities with different dominant species were controlled by water level (Chen et al., 2020). High elevation sites were dominated by *Triarrhena lutarioriparia* and *Carex cinerascens*, intermediate elevation sites were dominated by *Phalaris arundinacea* and *C. cinerascens*, and low elevation sites were dominated by *C. cinerascens* (Figures 2, S1).

2.2 | Study design and laboratory procedures

We set five blocks along the levee at approximately 500-m intervals. Within each block, we set one sampling transect in each lake, and there were 10 sampling transects in total. Along each sampling transect, there were six sampling sites from the levee to the waterline. The elevation of each sampling site was determined on 18 April 2017, with an electronic tachometer total station (RTK systems, S86, South Surveying and Mapping Instrument Company). There is a gauge station in Dahuchi Lake, and the real-time water level of Dahuchi Lake was available. For Chizhou Lake, we used the daily water level from the neighbouring Wucheng gauge station (distance <10 km to Chizhou Lake) that has a similar elevation.

We set a 1-m × 0.5-m quadrat at each sampling site in winter (December 8–10, 2016) and another neighbouring quadrat in spring (15–18 April 2017). We collected all above-ground plant materials in each quadrat. All live plant materials were divided into species, oven-dried to a constant mass at 70°C for 24 hr and then weighed to determine the biomass of each species. Above-ground biomass of all live plant materials in each quadrat were the total biomass of all species. In each quadrat, relative biomass of each species was determined as the percentages of species' biomass to AGB of all species.

To indicate the nutrient limitation status (Ostertag & Dimanno, 2016), we determined the leaf N and P contents of one dominant species, *C. cinerascens*. We randomly collected 10 individual plants of *C. cinerascens* in each quadrat and combined them into one sample. The leaf samples were ground and passed through an 80-mesh sieve (mesh size 177 μm), and total leaf N and P contents determined. Leaf N content was determined using the Kjeldahl acid-digestion method with an Alpkem autoanalyser (Kjektec System 1026 Distilling Unit), and leaf P content was analysed with the molybdenum blue colorimetric method with a UV/visible spectrophotometer (Beckman Coulter DU 800).

Total N and P contents have been widely used to examine wetland soil nutrients (Li et al., 2017; Schoolmaster & Stagg, 2018). Soil total N and P contents were significantly positively correlated with concentrations of dissolved N and P in soil pore water during the entire growing season in Poyang Lake (Wang et al., 2016) and in some other floodplain ecosystems (Bai et al., 2012). Moreover, some studies found that floodplain plant productivity was better predicted by particulate nutrients than by dissolved nutrients in floodwater (Keizer et al., 2018). Therefore, we determined soil total N and P contents as the measurements of soil nutrient availability. Meanwhile, total N and P content of soil was relatively stable during the end of the non-flooding period and the beginning of the non-flooding period (Wang et al., 2016) because soil N and P content was relatively high and sediment from flood water is the dominant sources of soil N and P in this area. Due to the relative stability of soil total N and P content during the non-flooding period, and the high correlation between soil nutrient content and concentrations of dissolved N and P in soil pore water, soil nutrient content measured once during the growing season would be highly correlated with soil nutrient availability over the entire growing season (Bai et al., 2012). To save labour costs, we determined the soil N and P contents in spring as the measurement of soil nutrient availability (Wang, Chen, et al., 2014; Wang, Han, et al., 2014). On 15–18 April 2017, we collected *c*. 100 g samples of topsoil (0–10 cm) in each quadrat by the soil core method. Soil samples were air-dried in the laboratory. The total N and P contents of the dry soil were determined by the same methods used for the leaf samples.

Given that flooding at different water depths might have different effects on plants, we considered four ranges of water depths (>0, >0.6, >1.2, >2.0 m), based on the average height of three dominant plant species (Figure S1a-d). The number of days at these four ranges of water depth was highly correlated in this area (Figure S1e). Meanwhile, zones with different plant communities in this area were mainly controlled by flooding duration (Chen et al., 2020). Therefore, flooding depth is not as important as duration. To simplify the analyses, flooding depth was not considered in the following data analyses, and flooding duration was defined as the number of days in a year at water depth >0 m (the site elevation was lower than the water level).

2.3 | Nutrient addition experiment

A nutrient addition experiment was carried out in the Nanji Wetland National Nature Reserve, which is also located in the Poyang Lake floodplain and 40 km from Dahuchi Lake. Along the lakeshore meadow, we selected two types of plant communities with different flooding durations. Plant communities with relatively shorter flooding durations (multi-year mean of flooding duration was 157 days) were dominated by *C. cinerascens*. Plant communities with relatively long flooding durations (multi-year mean of flooding duration was 185 days) were dominated by *C. cinerascens* and *Heleocharis valleculosa*.

In each type of plant community, we adopted a randomised block design with nine blocks and 36 5-m × 5-m plots in total. In each block, there were four nutrient addition treatments: control (no nutrient addition), N addition, P addition, and both N and P addition. N was added as commercial urea fertiliser at a rate of 10 g N m^{-2} $year^{-1}$; and P was added as commercial P_2O_5 at a rate of 2.5 g P m^{-2} $year^{-1}$. The nutrient addition rate was determined based on the nutrient input rate of Poyang Lake (Wang, Chen, et al., 2014; Wang, Han, et al., 2014). Nutrients were added to each plot by hand in late February and late October, the beginning of the growing seasons in spring and in winter, respectively.

We set a 0.5-m × 1-m quadrat at each sampling site in spring (20–25 March) and in winter (8–10 November) in 2017. We collected all plant materials in each quadrat. All live plant materials were separated by species and oven-dried to a constant mass at 70°C for 24 hr and then weighed to determine the AGB.

2.4 | Data analyses

A paired *t*-test was used to test the effects of sampling season on AGB, the biomass of the 3 dominant species, leaf N and P contents and N:P ratio of *C. cinerascens*. We carried out stepwise regression analysis using AGB as the dependent variable and flooding duration, soil N and P contents as the independent variables. Given that AGB reached its peak value at a flooding duration of approximately 220 days, we divided the flooding duration gradient (130–350 days) into two subgroups: 130–220 days and 220–350 days. For each subgroup and the whole flooding duration gradient, we carried out stepwise regression analysis to test the effects of flooding duration and soil nutrients (N and P) content on AGB, respectively, in winter or in spring. Given that soil N and P content are highly correlated ($r = 0.80$, $p < 0.001$), to address the collinearity between soil N and P content in the stepwise regression analysis, we carried out principal component analysis for these two variables and used the first principal component (explaining 71% of the total variance) as the index of soil nutrient content.

The AGB response ratio to nutrient addition was calculated as AGB in the nutrient addition treatment relative to the mean value of AGB in the control treatment. Repeated measures analyses with PROC MIXED, a mixed linear model, were carried out for the AGB response ratio to nutrient addition, with season, nutrient addition treatment and their interactions as fixed effects.

All statistical analyses were performed using SAS Version 9.0 (SAS Institute).

TABLE 1 Effects of season on different variables using a paired *t*-test

Variable	*t*-value	*p*-value
Above-ground biomass	6.46	<0.001
Biomass of *Triarrhena lutarioriparia*	1.40	0.166
Biomass of *Carex cinerascens*	4.62	<0.001
Biomass of *Phalaris arundinacea*	4.21	<0.001
Leaf N content of *C. cinerascens*	3.16	0.005
Leaf P content of *C. cinerascens*	2.15	0.044
Leaf N:P ratio of *C. cinerascens*	0.31	0.758

3 | RESULTS

3.1 | Response of plant biomass to flooding duration

Sampling season had significant effects on AGB, the biomass of *C. cinerascens* and *P. arundinacea*, and the leaf N and P contents of *C. cinerascens*. There was, however, no significant effect on the biomass of *T. lutarioriparia* and leaf N:P ratio (Table 1). Above-ground biomass and flooding duration had a negatively linear correlation in winter but a quadratic relationship in spring (Figure 3a,b). The annual total AGB had no significant relationship with flooding duration (Figure 3c). Above-ground biomass in spring was negatively ($r = -0.40$, $p = 0.001$) correlated with AGB in winter and positively ($r = 0.72$, $p < 0.001$) correlated with the annual total AGB. Above-ground biomass in winter was positively ($r = 0.35$, $p = 0.007$) correlated with the annual total AGB. Litter coverage decreased with flooding duration in both winter and spring (Figure S2).

The biomass of the three dominant species accounted for 93.7% of the community AGB on average. The biomass of *T. lutarioriparia* had a broken-stick relationship with flooding duration in both spring and winter, and remained low when the flooding duration was >140 days (Figure S3a,d). The biomass of *C. cinerascens* decreased with flooding duration in winter but increased with flooding duration in spring (Figure S3b,e). The biomass of *P. arundinacea* had a quadratic relationship with flooding duration both in winter and in spring, and peaked when the flooding duration was approximately 220 days (Figure S3c,f).

3.2 | Relationship between soil nutrient content and plant biomass

The soil total N content, total P content, and N:P ratio had a quadratic relationship with flooding duration, and peaked when the flooding duration was approximately 220 days (Figure 3d–f). The AGB and soil N and P contents were negatively correlated in winter, while positively correlated in spring (Figure 4). The slope of the AGB–soil N content relationship differed significantly ($p < 0.05$) between the two subgroups with different flooding durations in winter and in spring (Figure 4a,b).

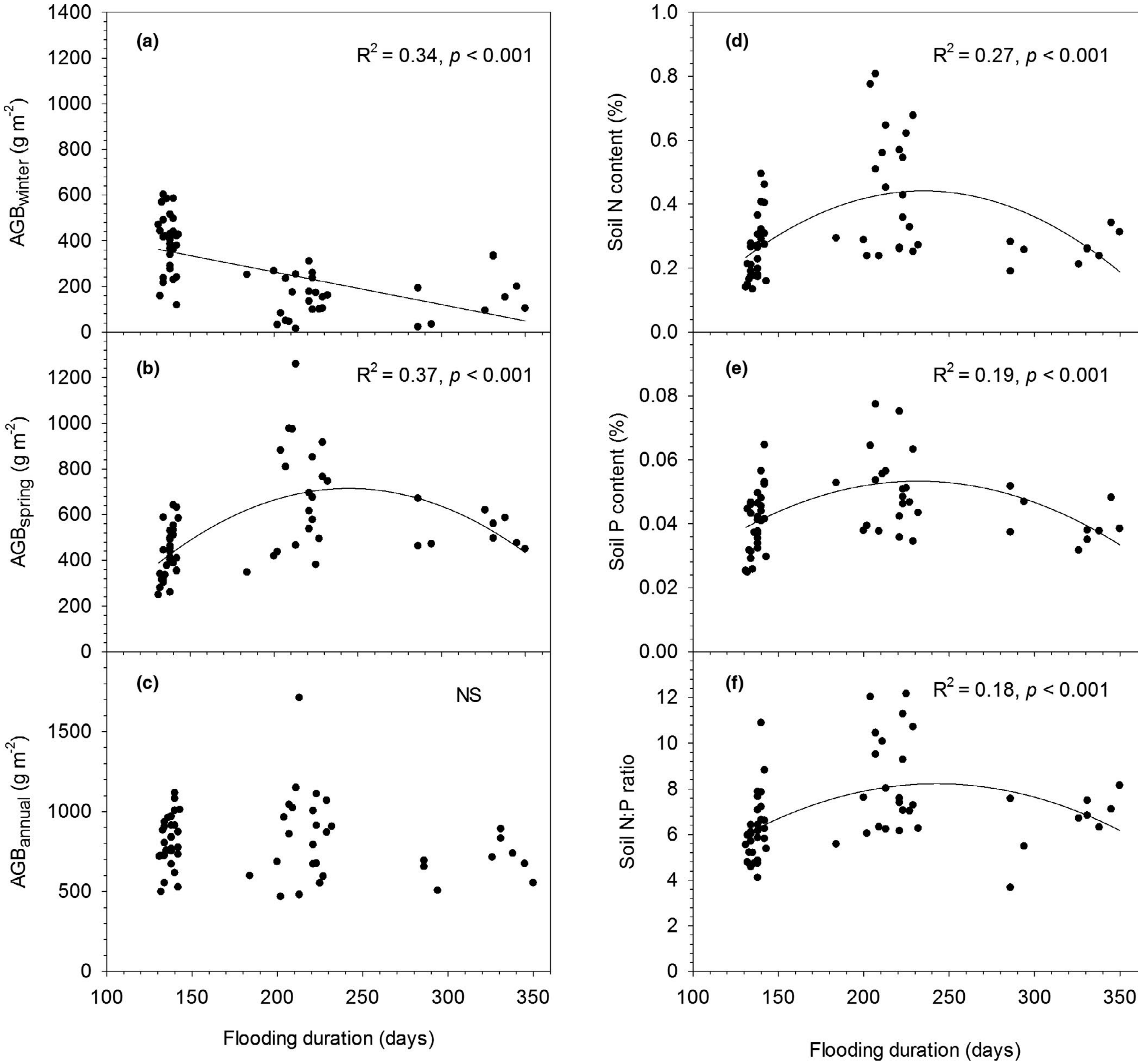

FIGURE 3 Relationship between flooding duration (at water depth >0 m) and (a) above-ground biomass (AGB) in winter of year 2016, (b) AGB in spring of year 2017, (c) annual total AGB, (d) soil total N content, (e) soil total P content, (f) soil N:P ratio

The slope of the AGB–soil P content relationship differed significantly ($p < 0.05$) between the two subgroups with different flooding durations in spring, but did not significantly ($p > 0.05$) differ in winter (Figure 4c,d).

The annual total AGB significantly increased with the soil N content ($r^2 = 0.09$, $p = 0.013$) and soil P content ($r^2 = 0.09$, $p = 0.013$). The biomass of *T. lutarioriparia* significantly ($p < 0.05$) decreased with the soil N and P contents both in winter and in spring. The biomass of *C. cinerascens* had no significant ($p > 0.05$) correlation with the soil N and P contents either in spring or in winter. The biomass of *P. arundinacea* significantly increased with the soil N and P contents in both winter and spring ($p < 0.05$).

In winter, the leaf N and P contents of *C. cinerascens* increased with flooding duration, while the leaf N:P ratio decreased with flooding duration (Figure 5a–c). In spring, the leaf N content in spring increased linearly with flooding duration (Figure 5d), while the slope of the leaf N-flooding duration relationship (fitted by a linear model) was significantly lower in spring than in winter ($p < 0.001$). The leaf P content in spring increased linearly with flooding duration (Figure 5e), while the slope of the leaf P-flooding duration relationship was significantly lower in spring than in winter ($p < 0.001$). The leaf N:P ratio had a U-shaped relationship with flooding duration in spring (Figure 5f). In winter, the leaf N and P contents significantly decreased ($p < 0.001$), while the leaf N:P ratio significantly ($p < 0.05$) increased with AGB ($p < 0.05$). In spring, the leaf N and P contents significantly increased with AGB

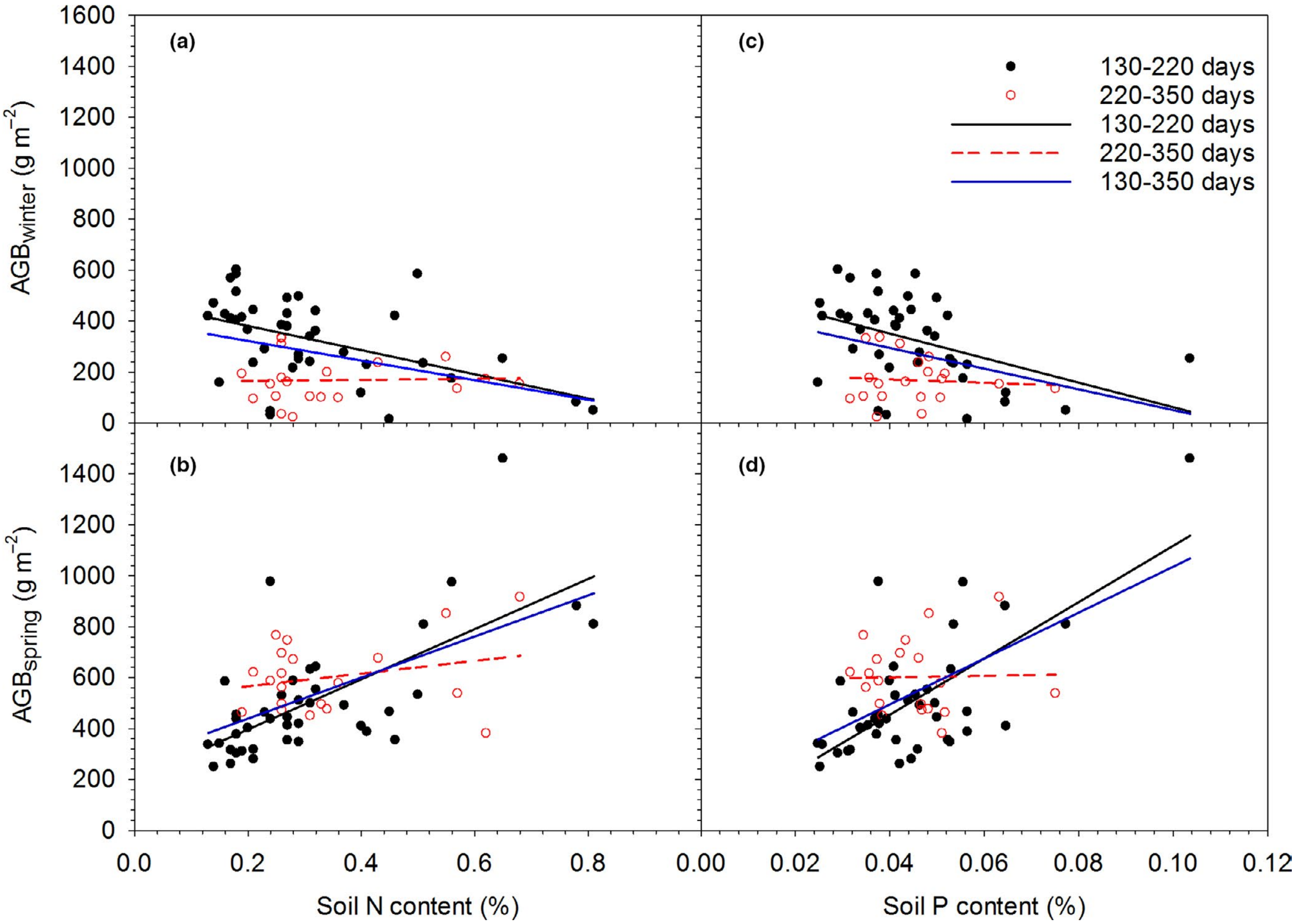

FIGURE 4 Relationship between soil nutrient content and above-ground biomass (AGB) in two seasons. Solid lines indicate that the fitted models were significant ($p < 0.05$) while dashed lines indicate that the fitted models were insignificant ($p > 0.05$)

($p < 0.05$), while leaf N:P ratio had no significant ($p > 0.05$) correlation with AGB ($p > 0.05$).

3.3 | Partitioned contributions of each factor to AGB

In winter, flooding duration explained 35% of the variance in AGB, while soil nutrient content (first principal component of soil N content and soil P content) explained only 9% of the variance (Table 2). In spring, flooding duration explained 5% of the variance in AGB, while soil nutrient content explained 37% of the variance (Table 2). For the subgroup with a flooding duration of 130–220 days, in winter, flooding duration explained 45% of the variance in AGB, while soil nutrient content had no significant contribution (Table 2). In the same subgroup, in spring, soil nutrient content explained 48% of the variance in AGB, while flooding duration explained 9% of the variance (Table 2). For the subgroup with a flooding duration of 220–350 days, neither flooding duration nor soil nutrient content contributed significantly to the variance in AGB in winter (Table 2). In the same subgroup, in spring, flooding duration explained 20% of the variance in AGB, while soil nutrient content had no significant contribution to the variance (Table 2).

3.4 | Above-ground biomass response ratio to nutrient addition

In communities with shorter flooding durations, the response ratio of AGB to nutrient addition was significantly higher in spring than in winter (Figure 6a). However, in communities with longer flooding durations, the nitrogen addition effect did not differ between the two seasons (Figure 6b). The response ratio of AGB to nutrient addition was significantly ($p = 0.001$) greater in communities with shorter flooding durations than in those with longer flooding durations in spring, but no significant variation ($p > 0.05$) was observed in either type of community in winter.

4 | DISCUSSION

The relationship between wetland plant biomass and flooding duration varied among different studies (Garssen et al., 2015, 2017;

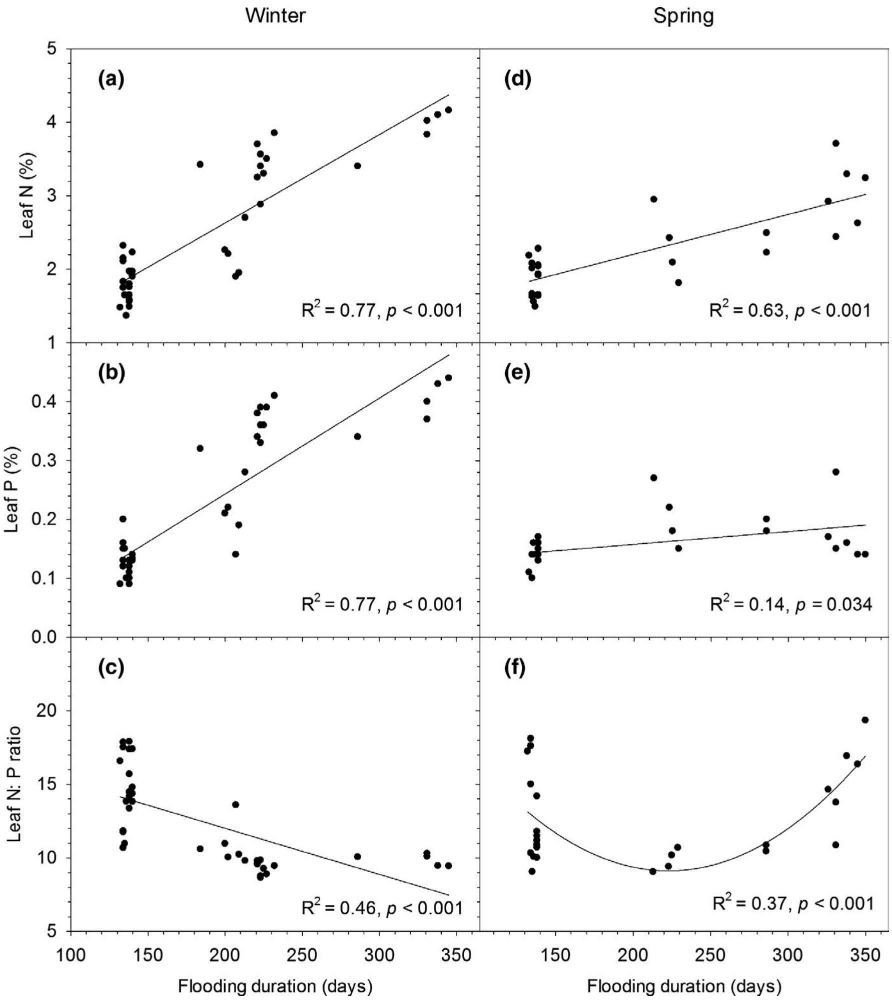

FIGURE 5 Relationship between flooding duration (at water depth >0 m) and the leaf N content, P content and N:P ratio of *C. cinerascens* in winter and in spring

TABLE 2 Partial r^2 of stepwise regression analysis for above-ground biomass (AGB)

	Flooding duration	Soil nutrient content[a]	Final model
Duration 130–350 days ($n = 60$)			
AGB_{winter}	0.34***	0.09**	0.43***
AGB_{spring}	0.05*	0.37***	0.42***
Duration 130–220 days ($n = 40$)			
AGB_{winter}	0.45***	ns	0.45***
AGB_{spring}	0.09**	0.48***	0.57***
Duration 220–350 days ($n = 20$)			
AGB_{winter}	ns	ns	ns
AGB_{spring}	0.20*	ns	0.20*

Note: ns, $p > 0.05$; *, $p < 0.05$; **, $p < 0.01$; and ***, $p < 0.001$.

[a] Soil nutrient content was the first principal component of the soil N content and P content.

Wang, Chen, et al., 2014; Wang, Han, et al., 2014). Our study showed that this relationship depended on many factors. Firstly, in our study, plant growth at the lowest elevations was limited by flood stress, whereas plant growth at higher elevations could be limited by soil nutrients. Therefore, along a flooding duration gradient ranging from 130 to 350 days, the AGB in spring had a quadratic relationship with flooding duration. When the scale of flooding duration gradient was relatively small, the relationship between AGB and flooding duration could be positive (Garssen et al., 2017), negative (Lan, Chen, et al., 2019), or not significant (Garssen et al., 2015). Secondly, previous studies in different sampling seasons showed different response patterns of AGB to flooding duration (Chen et al., 2002; Li et al., 2013; Lou et al., 2016; Megonigal & Day, 1992). Our results suggested that the relationship between AGB and flooding duration depended on season. Most existing studies, however, focus on one season (Garssen et al., 2015). Overall, the scale of flooding duration and the sampling season could significantly alter the relationship between flooding and wetland plant biomass. Previous studies, however, rarely considered these factors in their experimental design and data analyses.

Flooding duration could affect soil nutrient availability positively (Wright et al., 2015), negatively (Lan, Chen, et al., 2019), not significantly (Wang, Chen, et al., 2014; Wang, Han, et al., 2014), or show a quadratic relationships (e.g. our study). Diverse patterns of flooding–soil nutrient relationships could be attributed to multiple effects of flooding on soil nutrient cycling (Baldwin & Mitchell, 2000; Carmignani & Roy, 2017; Keizer et al., 2018; Noe et al., 2019). In our study area, flooding effects on soil nutrient availability were mixed.

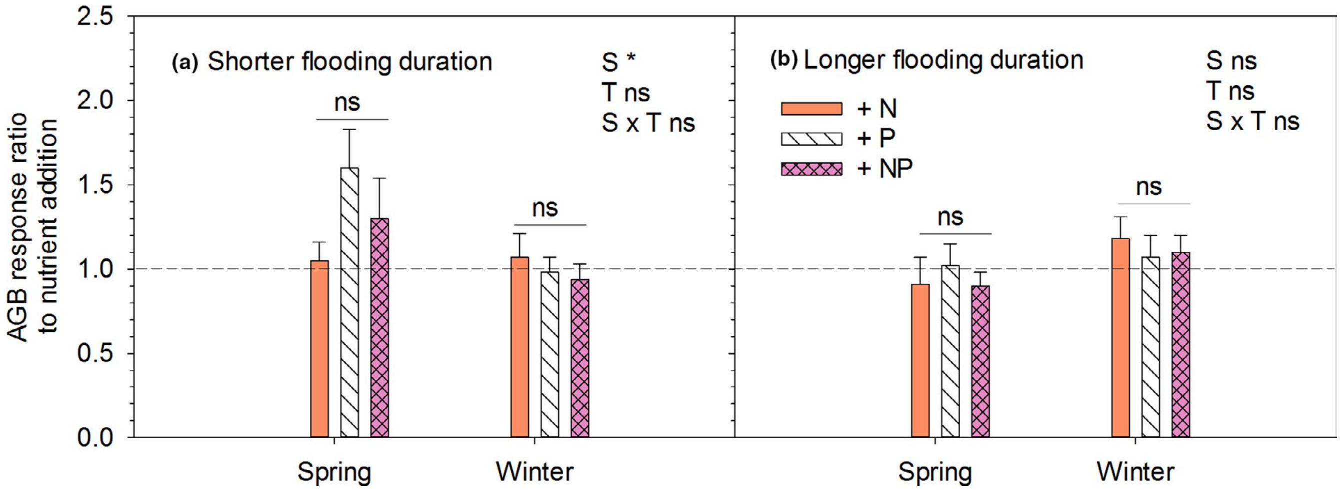

FIGURE 6 Above-ground biomass (AGB) response ratio to nutrient addition in spring and in winter of year 2017 for communities with (a) shorter and (b) longer flooding duration. Bars with the same letters were not significantly ($p > 0.05$) different based on Duncan's multiple range tests reported from one-way ANOVA, and ns indicates that all bars within the same group were not significantly different. Note: ns, $p > 0.05$; *, $p < 0.05$

On the one side, litter biomass, which was an important source for soil nutrient (Baldwin & Mitchell, 2000), decreased with flooding duration. On the other side, although we did not determine the sedimentation rate, the nutrients input through sedimentation usually increased with flooding duration in other floodplain systems (Keizer et al., 2018). Therefore, soil nutrient content peaked at the intermediate flooding duration in our study.

Our study found significant nutrient limitation to AGB, and further supported the hypothesis that nutrient limitation decreased with flooding duration. At the community level, AGB of communities with shorter flooding durations showed greater responses to nutrient addition. Meanwhile, the correlation between soil nutrient content and AGB was more significant at short flooding duration than at long flooding duration. At the species level, flooding usually favours species with traits related to flooding tolerance and greater leaf nutrient contents (Fischer et al., 2016; Lan, Huang, et al., 2019). In our study, longer flooding duration favored *P. arundinacea* with greater leaf nutrient contents over *T. lutarioriparia*. At the intra-species level, consistent with previous studies (Lan, Huang, et al., 2019; Li et al., 2017), leaf nutrient content of *C. cinerascens* increased with flooding duration, suggesting a decrease in the importance of nutrient limitation.

Our results supported the prediction that nutrient limitation was greater in spring than in winter. Firstly, the leaf N and P contents, as an index of nutrient limitation (Ostertag & Dimanno, 2016), were greater in winter than in spring in our study. Secondly, AGB was positively correlated with the soil nutrient content in spring, while it was negatively correlated with the soil nutrient content in winter. Thirdly, the response of AGB to nutrient addition was significantly higher in spring than in winter. In all, consistent with some studies in terrestrial ecosystems (González-García & Martín Martín, 2017), the effects of soil nutrient availability on wetland ecosystems might depend on the season because nutrient limitation varied with season.

Overall, our study supported the stress gradient hypothesis because there was a shift between flooding stress and nutrient limitation along the flooding duration gradient and between different seasons during the non-flooding period. In previous studies, decreased flooding stress could increase plant biomass, which would enhance nutrient storage and nutrient limitation of plant communities (Lan, Chen, et al., 2019; Olde Venterink et al., 2001; Palpurina et al., 2019). In our study, however, the leaf N and P content increased with AGB in spring, suggesting that nutrient limitation was negatively correlated with AGB. Meanwhile, plant productivity could sometimes increase with enhanced environmental stress (Schoolmaster & Stagg, 2018). Therefore, it is possible that the shift between flooding stress and nutrient limitation is not triggered by productivity.

There are extensive studies on relative importance of N versus P to plant growth with the index of leaf N:P ratio (Güsewell et al., 2003; Ostertag & Dimanno, 2016; Yan et al., 2017). In our study, response patterns of leaf N:P ratio to flooding duration differed between two seasons during the non-flooding period, suggesting that the relative importance of N versus P along flooding duration depended on season. In the nutrient addition experiment, N addition significantly increased AGB in spring, indicating N limitation of AGB in Poyang Lake (Lan, Chen, et al., 2019). Addition of P, however, had no significant effect on AGB, which might be attributed to a relatively low proportion of available P to soil total P (Wang et al., 2016). Meanwhile, the response pattern of leaf N:P ratio to flooding duration differed from that of soil N:P ratio, suggesting that soil nutrient stoichiometry was not the only limiting factor for leaf N:P ratio (Güsewell & Koerselman, 2002). Moreover, leaf N:P ratio was negatively correlated with metabolic activities and growth rate (Rivas-Ubach et al., 2012). In winter, leaf N and P contents increased while N:P ratio decreased with flooding duration, suggesting that plants adopted a strategy of greater metabolic and growth rates in response to enhanced flooding stress (Colmer & Voesenek, 2009). In spring, leaf N:P ratio showed a U-shaped response to flooding duration, suggesting that peak growth rate occurred at the intermediate flooding duration, which was consistent with the response pattern of AGB.

Flooding duration could affect AGB via both direct and indirect pathways (Garssen et al., 2017; Lan, Chen, et al., 2019). In our study, the relative importance of direct and indirect pathways depended on season. As discussed previously, the importance of nutrient limitation was greater in spring than in winter. Moreover, the direct effects of flooding duration might decrease over time during the non-flooding period (Chen & Xie, 2009), and as a result, the effects were lower in spring than in winter in our study. Furthermore, the relative importance of each pathway depended on flooding duration. At flooding durations of 130–220 days, the direct flooding effect on AGB was much lower than the effect of soil nutrients in spring. However, at flooding durations of 220–350 days, direct flooding effects were more important than soil nutrient effects on AGB in either winter or spring.

There are some uncertainties in interpreting our results. Although total N and P contents remained relatively stable during the non-flooding period, the concentration of dissolved N and P in soil pore water might vary with season and flooding duration (Garssen et al., 2017). These variations might weaken the explanation of variations in AGB based on soil total N and P content. However, as discussed above, the conclusions based on soil total N and P contents (e.g. nutrient limitation varied with season and flooding duration) were also supported by the results relating to leaf nutrient contents and nutrient addition effects. Meanwhile, in Poyang Lake, concentrations of dissolved soil nutrients were highly positively correlated with total soil nutrient contents (Wang et al., 2016). Some studies further found that particulate nutrients were more important for floodplain wetland biomass than dissolved nutrients (Keizer et al., 2018). Therefore, the main conclusions of our study are robust based on this evidence.

Our findings have several implications for understanding the ecological impacts of global climate change and better management of wetland ecosystems. Firstly, climate change and human activities are projected to change the flooding regimes of most wetlands (Goodwin et al., 2014; Hirabayashi et al., 2013; Munoz et al., 2018). We expect that wetland plant biomass in these areas will show diverse responses to altered flooding regimes, depending on the season, scale of flooding duration, and soil nutrient availability. Secondly, given that many wetland ecosystems are still experiencing nutrients enrichment (Huang et al., 2019; Sinha et al., 2017), changes in flooding regimes and nutrient enrichment will interactively affect wetland ecosystems. Thirdly, water level regulation is important for wetland ecosystem management and conservation (Keddy, 2010; Poff & Olden, 2017). In our study, wetland plant biomass and soil nutrient content had non-linear relationships with flooding duration, indicating complex implications of water level regulation (Garssen et al., 2017).

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

AUTHOR CONTRIBUTIONS

Z.C. Lan, Y.S. Chen, and J.K. Chen designed the study. Z.C. Lan and R.C. Shen analysed data. Z.C. Lan, Y.J. Cai, H. Luo, B.S. Jin, and J.K. Chen contributed to the manuscript and revisions.

DATA AVAILABILITY STATEMENT

Data are available from the Institute of Watershed Ecology, Nanchang University (lanzhichun@ncu.edu.cn).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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