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Temporal and spatial variations of soil physicochemical properties, vegetation, and soil enzyme activities in a riparian zone

하천변 토양 환경, 식생, 토양 효소 활성의 시공간적 변동

2020 년 2 월

서울대학교 대학원

과학교육과 생물전공

박 혜 경

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Abstract

Temporal and spatial variations of soil physicochemical properties, vegetation, and soil enzyme activities in a riparian zone

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In the riparian zone, dynamic and complex feedback among soil, vegetation and soil microbes occur, and variations of hydrological regime as a result of flooding alter such feedback, which can also change biogeochemical cycle of the riparian zone. The objectives of this study were to determine how soil physicochemical properties, vegetation, and soil biological properties vary among different topography, especially elevation above the water level and distance from the river channel, with time, to identify the relationships among soil biological properties, soil physicochemical properties and vegetation, comprehensively, and to identify the governing factors determining soil biological properties. In a riparian zone of Namhan river in South Korea, total of 30 quadrats were classified into three different groups

according to elevation (Low, Middle, and High). Soil physicochemical properties, vegetation, and soil biological properties (soil enzyme activities, soil microbial biomass and CO_2 efflux) were analyzed before and after flooding season (pre-flooding: June, post-flooding: August and October). In the riparian zone, there were temporal and spatial variations in soil physicochemical properties and vegetation. Flooding created hydrological gradient along the elevation, and variations of hydrological regime, and consequently the variations in soil moisture content appear to be the most important factors that influence the system of the riparian zone. The activities of β-glucosidase, β-N-acetylglucoasminidase, acid phosphatase, and alkaline phosphatase showed decreasing trends with higher elevations. However, there was only a temporal variation in microbial biomass, and there were no significant temporal and spatial variations in CO_2 efflux. Individual enzyme activity responded differently to flooding. Soil moisture content was a major factor influencing soil biological properties both in pre- and post- flooding, and flooding altered the primary factors governing soil biological properties. The other main factors governing soil biological properties were organic matter content, nutrient availability, especially P limitation, and aboveground biomass. Based on these results, I conclude that variations of soil physicochemical properties, vegetation, and soil enzyme activities in the riparian zone are due to comprehensive changes in dynamic interactions between biotic and abiotic factors caused by flooding rather than solely due to the effects of flooding.

Keywords : Biogeochemical cycle, Elevation, Flooding, Hydrological regime, Soil microbes, Soil moisture content

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Contents

Abstract i

1. Introduction 1

2. Materials and Methods 7

3. Results 17
3.1 Soil physicochemical properties 17
3.2 Vegetation 21
3.3 Relationship between vegetation and soil physicochemical properties 27
3.4 Soil biological properties 31
3.5 Relationship between soil biological properties and soil physicochemical properties and vegetation 36

4. Discussion 41
4.1 Temporal and spatial variations in soil physicochemical properties 41
4.2 Temporal and spatial variations in vegetation 45
4.3 Effects of soil physicochemical proeprties on vegetation 49
4.4 Temporal and spatial variations in soil biological properties . 50
4.5 Effects of soil physicochemical properties and vegetation on soil biological properites 52
4.6 Syntheesis 56

5. Conclusions 59

Reference 60

Abstract in Korean 77

Contents of Table

Table 1. The effects of elevation and time on physicochemical properties using repeated measures ANOVA (rmANOVA) or Friedman's test **18**

Table 2. Variations of soil physicochemical properties under different elevations during the study period (mean±SE) **20**

Table 3. Species list in the studied riparian zone **24**

Table 4. The effects of elevation and time on soil biological properties using repeated measures ANOVA (rmANOVA) or Friedman's test **32**

Table 5. Correlation coefficients between soil biological properties and soil physicochemical properties and vegetation **40**

Contents of Figure

Figure 1. Conceptual diagram of research qustions. **6**

Figure 2. The study site and schematic diagram of field survey. **7**

Figure 3. Daily precipitation and daily mean air temperature from January to October 2019 at the study site. **8**

Figure 4. Discharge and water level from May to October 2019 at the study site. **9**

Figure 5. Distribution patterns of aboveground biomass (a, b, c) and species diversity (d, e, f) along the gradient of elevation. **22**

Figure 6. Systematic diagram of bisect and dominant species in pre-flooding (a), post-flooding 1 (b), and post-flooding 2 (c). **26**

Figure 7. TWINSPAN dendrogram of pre-flooding (a), post-flooding 1 (b), and post-flooding 2 (c). **28**

Figure 8. Redundancy analysis (RDA) ordination of vegetation quadrats (*n*=30) and soil physicochemical variables (arrows) for pre-flooding (a), post-flooding 1 (b), and post-flooding 2 (c). **30**

Figure 9. Variations of soil biological properties under different elevations during the study period (mean±SE). **34**

Figure 10. The stoichiometry of soil enzyme activities under different elevations during the study period (mean±SE). **35**

Figure 11. Redundancy analysis (RDA) of soil biological properties (soil enzyme activities, microbial biomass, and CO_2 efflux) and soil physicochemical properties and vegetation in pre-flooding (a), post-flooding 1 (b), and post-flooding 2 (c). **37**

Figure 12. Schematic diagram of the relationships between flooding, soil physicochemical properties (pH, EC, soil moisture content, organic matter content, nutrient availability, and soil particle distribution), vegetation traits (vegetation structure and aboveground biomass), and soil microbes. **58**

1. Introduction

The riparian zone is hydrological and biogeochemical ecotone of terrestrial and aquatic ecosystems. The riparian zone is unique in interactions with adjacent ecosystems and provides a wide range of ecosystem services. It plays an important role in maintaining biodiversity by providing habitats for plants and animals, improving water quality, and stabilizing stream banks against floods (Whiting and Pomeranets 1997). In the riparian zone, the lateral exchange of water, materials, energy, and biota is mainly via floods (Pinay and Decamps 1988, Brunet et al., 1994, Walling and He 1998).

Flooding, the periodic change between wet and dry conditions as a result of fluctuations in river flow, alters hydrological regime which is a pivotal driving force developing and maintaining the system of the riparian zone in a dynamic equilibrium (Ward 1989). On the one hand, variations of hydrological regime have significant effects on soil physicochemical properties and vegetation (Xiu et al. 2015), thus affect microbial community structure, abundance and function (Boz et al. 2013). On the other hand, different hydrological regime can also directly lead to shifts in soil microbes (Gutknecht et al. 2006), leading to changes in soil nutrient dynamics (Hefting et al. 2004), and as a consequence affect vegetation (Lange et al. 2015). In other words, flooding enhances hydrological dynamics in the riparian zone, thereby changing feedbacks among soil physicochemical properties, vegetation and microbial properties.

The characteristics of flooding such as frequency, duration, and magnitude, however, are often influenced by the topographical differences in the riparian zone.

For example, low-lying areas have a longer water residence time compared to high-lying areas. The gradient in hydrological regime from low- to high-lying areas creates temporal and spatial heterogeneity of vegetation and soil physicochemical properties including soil moisture content, soil redox potential, nutrient availability and organic matter content (Steiger et al. 2005, Polvi et al. 2011).

Based on these dynamic interactions between biotic and abiotic factors, the riparian zone can contribute to regional and global biogeochemical cycle. For instance, the riparian zone regulates the transfer of nutrients and organic matters (Pinay and Decamps 1988), and acts as a sink or source of nutrients depending on various factors, such as hydrological regime, soil physicochemical properties or topography (Hill 1996). Materials transported from upland accumulate in the riparian zone until they flow into the river or return to the atmosphere, and flooding facilitates such fluxes. Amounts of nutrients and organic matters transported and retained depend on soil physicochemical properties such as soil moisture content, soil particle distribution and soil redox potential (Pinay and Decamps 1988). Besides, temporal and spatial variations of plant community structure and biomass due to flooding induce the differences in nutrient uptake or release to soil in litter fall and root turnover. That is, there are temporal and spatial variations in biogeochemical cycle in response to hydrological regime (Takatert et al. 1999, Baldwin and Mitchell 2000, Wolf et al. 2014), topography (Xiong et al. 2015), soil physicochemical properties (Geisseler and Horwath 2009), and vegetation (Vought et al. 1994, Wagner et al. 2015).

Among various soil biological properties, there are several factors used to understand the biogeochemical cycle of the riparian zone. First of all, soil microbes play an important role in the biogeochemical cycle, such as organic matter decomposition and nutrient cycling. Soil microbes secrete soil enzymes that act as

catalysts for some biogeochemical processes, particularly degrading macromolecular compounds by hydrolysis or oxidation to simple compounds that can be easily taken up by soil microbes and plants (Sinsabaugh et al. 1991, Singh and Kumar 2008). Therefore, soil enzyme activity is widely used as an indicator of microbial community function (Caldwell 2005). Microbial biomass, defined as living component of soil organic matter, acts as a sink or source of nutrients (Inubushi and Acquaye 2004). Given that immobilization of nutrients in microbial biomass depends on amount of organic matters and available nutrients, microbial biomass is an important indicator of the changes in quantity and quality of organic matters and nutrients. Moreover, microbial biomass which is sensitive to soil changes may help understanding the effects of flooding on microbial community (Kaiser et al. 1992). Lastly, soil CO_2 emission, originated from plant roots or heterotrophs (Kuzyakov and Larionova 2005), is a key step for biogeochemical processes, especially in the context of carbon cycling.

Previous studies suggested that soil biological properties in the riparian zone were significantly related to temperature (Zhou et al. 2013), hydrological regime (Bardgett and Shine 1999, Geng et al. 2017), soil moisture content (Van Gestel et al. 1996, Goodrick et al. 2016), and nutrient availability (Hill et al. 2018). Although there have been some studies on the effects of flooding on biogeochemical cycle, most were carried out at the level of mesocosm experiments, which simulated hydrological regime, such as frequency, duration and magnitude of flooding (Anderson and Mitsch 2005, Mentzer et al. 2006, Smith and Jacinthe 2014). The Riparian zone, however, is an open system where complex and dynamic interactions with floods occur (Baldwin and Mitchell 2000). Moreover, the occurrence of extreme droughts and floods has gradually increased as a result of climate change (Kundzewicz et al. 2010). Therefore, an attempt to explain the responses of natural flooding in the field is

required.

Furthermore, field study in the riparian zone is necessary in terms of the need for consideration of the role of plants in biogeochemical cycle. Plants are known to play a critical role in biogeochemical cycle. Plants can influence microbial community structure by releasing enzymes, exudates and oxygen into the rhizosphere affecting microbial density or activity. Plants regulate nutrient dynamics through nutrient uptake or release. Amount, structure, and nutrient contents of organic molecules released to soil through root turnover or litter fall vary according to plant species, and quantity and quality of nutrients contributed to soils also differ (Barling and Moore 1994, Caravaca et al. 2005). In addition, nutrient uptake of plants leads to heterogeneous distribution of nutrients. Vegetation in the riparian zone, however, shows dynamic variations due to flooding (Hupp and Osterkamp 1996), and vegetation traits that reflect responses to environmental changes include species composition and distribution patterns, species diversity or richness, and biomass. Given that, temporal and spatial variations of vegetation induced by flooding would alter biogeochemical cycle in the riparian zone. Accordingly, vegetation traits are needed to be considered along with soil physicochemical properties to understand biogeochemical cycle in the riparian zone.

Although temporal and spatial variations in soil biological properties in the riparian zone have been assessed in many studies (Balasooriya et al. 2008, Jia and Liu 2017, de Sosa et al. 2018, Qu et al. 2019), each study showed different results depending on the conditions. Macé et al. (2016) reported soil enzyme activities increased with flooding magnitude, and flooding effects were enhanced at higher plant diversity, whereas Geng et al. (2017) demonstrated individual enzyme activity responded differently to various flooding frequency and duration. Ou et al. (2019) reported flooding altered principal factors governing soil enzyme activities, while the

only governing factor of microbial community was C/N ratio regardless of flooding. In contrast, Wang et al. (2019) showed that hydrological condition and available nutrient level determined microbial community structure and function.

This inconsistency may be attributed to the fact that few studies have taken into account interactions between interrelated properties, such as topography, soil physicochemical properties, vegetation, and microbial properties. In the riparian zone, dynamic and complex feedback among soil, vegetation and soil microbes occur. Moreover, variations of hydrological regime as a result of flooding alter such feedback, which can also change biogeochemical cycle of the riparian zone. A number of studies have been carried out on biogeochemical properties, such as soil enzyme activities, according to soil physicochemical properties or hydrological regime, but few studies have considered the effects of several factors on biogeochemical properties comprehensively. Furthermore, the presence of plants is known to affect biogeochemical cycle, but little is known about the effects of temporal and spatial variations of vegetation traits caused by flooding, such as plant community structure, species composition and distribution, biomass, species richness and diversity.

The aim of this study was to provide a comprehensive understanding of temporal and spatial variations of biogeochemical cycle due to flooding in the riparian zone (Figure 1). The specific objectives were 1) to determine how soil physicochemical properties, vegetation, and soil biological properties vary among different topography, especially elevation above the water level and distance from the river channel, with time, 2) to identify the relationships among soil biological properties, soil physicochemical properties and vegetation, and 3) to identify the governing factors determining soil biological properties considering soil physicochemical properties, vegetation, hydrological regime comprehensively.

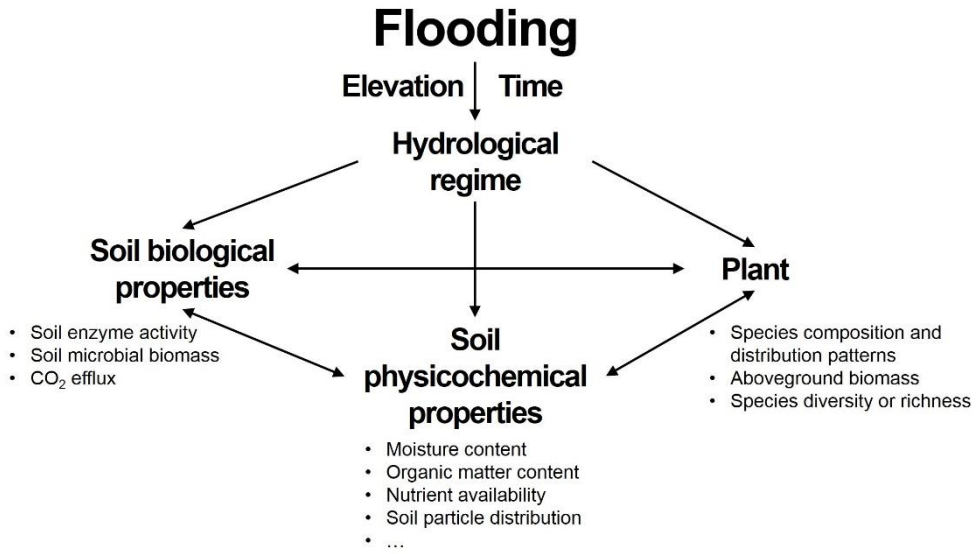


Figure 1. Conceptual diagram of research questions.

2. Materials and Methods

2.1 Study site and field survey

Field survey was conducted in a riparian zone of Namhan river in Yeoju City, Gyeonggi Province, South Korea (37°26'N, 127°30'E) (Figure 2). The site received 936 mm of rainfall between January and October 2019, and the temperature ranged from -6.4°C to 30.5°C with the average temperature of 14.5°C (Figure 3). The climate in this area is monsoonal with high rainfall during the summer in July (total rainfall 215.1 mm) and August (total rainfall 225.6 mm), which is almost 47% of the annual precipitation.

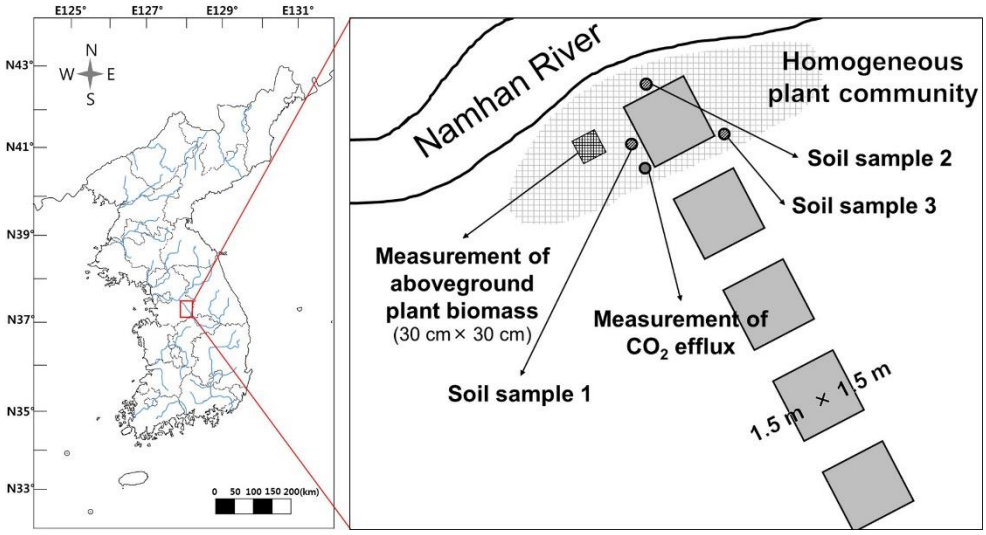


Figure 2. The study site and schematic diagram of field survey.

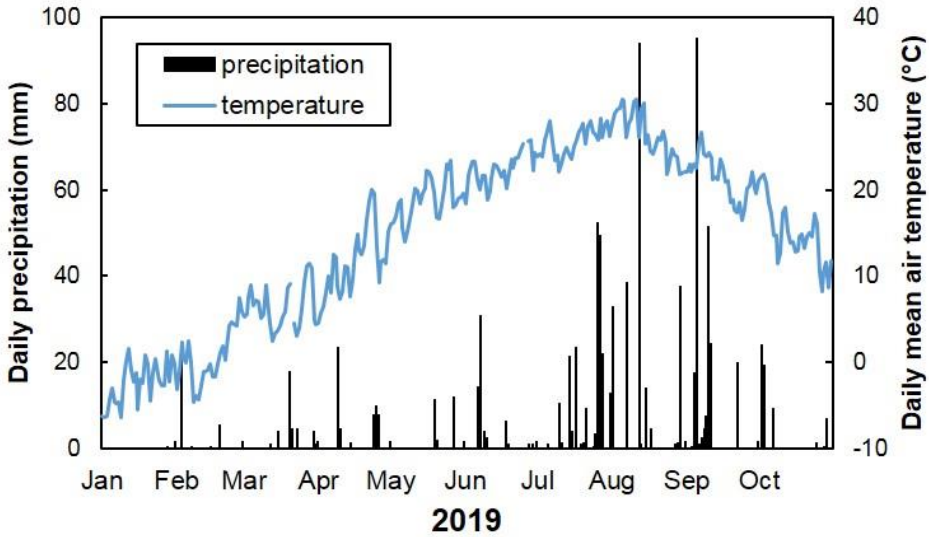


Figure 3. Daily precipitation and daily mean air temperature from January to October 2019 at the study site.

In the study site, six replicate permanent line transects were established perpendicular to the river channel, and five quadrats of 2.25 m^2 (1.5 m × 1.5 m) were established within each line transect (total 30 quadrats) (Figure 2). For each quadrat, distance from the river channel and elevation above the water level were measured. The distance and the relative elevation of a total of 30 quadrats varied from 0 to 10.5 m and 0 to 116 cm, respectively. Quadrats were classified into three different groups (hereafter these are referred to as low, middle, and high elevation) according to their dominant vegetation cover. Low elevation (n=6), located adjacent to the river channel (0 cm to the river), was dominated by obligate wetland plants, such as *Zizania latifolia*. Middle elevation (n=10), located < 26 cm above the water line and < 6.5 m from the river channel, was mostly dominated by *Polygonum thunbergii*. High elevation (n=14), where distinctive plants dominated according to season, located 28-116 cm above the water line and 5.5-10.5 m from the river channel.

Field survey was conducted prior to flooding (pre-flooding; 4-5 June 2019)

and after flooding (post-flooding 1; 26-27 August 2019 and post-flooding 2; 7 October 2019) at the same quadrats. In pre-flooding, total monthly rainfall was only 25.5 mm and there were almost no variations in water level or discharge. In contrast, before post-flooding 1, intense rainfalls occurred particularly from 26 July to 1 August (total rainfall 170.1 mm) and 7 to 12 August (total rainfall 132.8 mm). In post flooding 2, there were relatively moderate rainfalls repeated: from 4 to 5 September (total rainfall 112.5 mm), 10 to 11 September (total rainfall 76.0 mm) and 2 to 3 October (total rainfall 43.5 mm) (Figure 4).

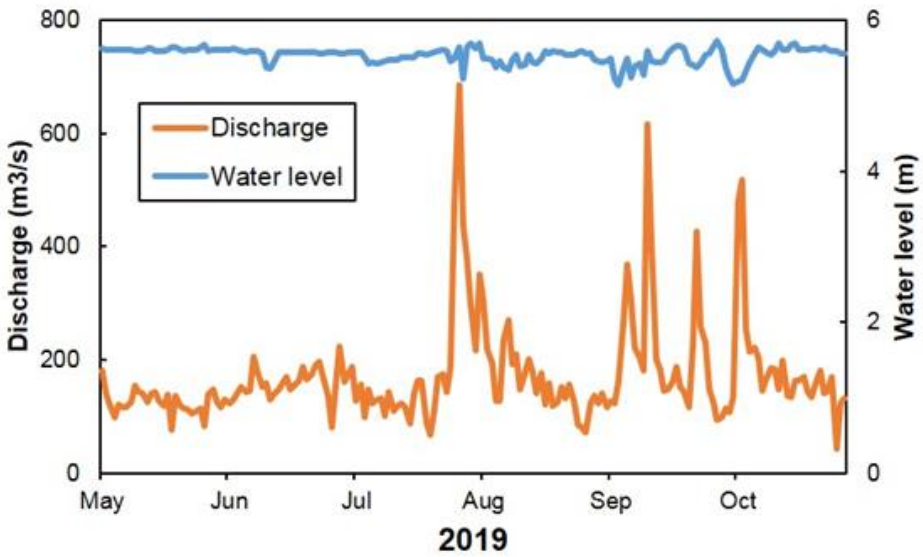


Figure 4. Discharge and water level from May to October 2019 at the study site.

Average height, density, and coverage of every species emerged in 1.5 m x 1.5 m quadrats were surveyed. Some immature or juvenile plants were identified only to the family level. According to the literature by Choung et al. (2012), plant species were classified into five categories based on the frequency of each species in its habitats as follows: obligate upland plant (OBU), facultative upland plant (FACU), facultative plant (FAC), facultative wetland plant (FACW), and obligate wetland plant (OBW). The obligate and facultative wetland plants were classified into hygrophyte and emergent based on the degree of wetness of their habitats. In each quadrat, aboveground biomass was determined by harvesting vegetation samples from 30 cm x 30 cm quadrat and oven-dried at 60°C for over 48 hours.

2.2 Soil CO_2 efflux

Soil CO_2 efflux was measured using an automated soil CO_2 flux system (LI-8100; LI-COR Biosciences Inc., Lincoln, NE, USA). Soil CO_2 efflux is measured by monitoring the changes in CO_2 concentration inside the chamber by using an infrared gas analyzer. PVC soil collars were inserted into the soil, and the chamber was placed on the soil collars. Living plants inside the soil collars were removed before each measurement of soil CO_2 efflux to eliminate aboveground plant respiration. To minimize daily variation in soil CO_2 efflux, measurements were made between 9:00 a.m. and 12:00 p.m. Soil temperature (°C) and gravimetric soil moisture content (% in volume) were measured adjacent to each collar using probes connected to LI-8100 at the same time of soil CO_2 efflux measurement.

2.3 Soil sampling

As soils were not homogeneous within a quadrat, three soil samples at a depth of 0-20 cm from the soil top layer were randomly collected from each quadrat, obtaining a total of 90 soil samples for each survey period. Prior to analysis, they were sieved through a 2-mm mesh (standard sieve #10) to remove any plant material or gravel, mixed thoroughly, and stored at 4°C. Each 100 g of subsample was dried for soil texture analysis.

2.4 Soil physicochemical properties

The soil moisture content was measured based on the weight loss of soil dried at 105°C in an oven for over 48 hours, and the organic matter content was determined by loss of ignition (LOI) at 550°C for 4 hours (Boyle 2004). The soil pH and electric conductivity (EC) were measured in a 1:5 (w/v) soil/deionized water suspension solution using a pH meter and a conductivity meter, respectively. Soil texture was determined using the hydrometer method and the soil texture triangle of USDA (Carter 1993).

NO_3-N and NH_4-N were extracted with 2 M KCl solution and concentrations were measured using hydrazine method (Kamphake et al. 1967) and indo-phenol method (Murphy and Riley 1962), respectively. PO_4-P concentration was determined using ascorbic acid reduction method (Solorzano 1969) after extraction with Bray No. 1 solution (Bray and Kurtz 1945). Exchangeable cation concentra-tions (K^+, Na^+, Ca^{2+} and Mg^{2+}) were measured using an atomic absorption spectrometer (model AA240FS; Varian, USA) after extraction with 1 N ammonium acetate solution (Allen et al. 1974).

2.5 Soil enzyme activities

Four soil enzymes representative of important nutrient cycles were chosen for this study: β-glucosidase (BG, EC 3.2.1.21), β-N-acetylglucoasminidase (NAG, EC 3.2.1.30), acid phosphatase (ACP, EC 3.1.3.2), and alkaline phosphatase (ALP, EC 3.1.3.1). BG is carbon-related enzyme, which is involved in microbial degradation of cellulose to glucose (Klose and Tabatabai 2002). NAG is nitrogen-related enzyme, which is related to the mineralization of organic nitrogen polymers, such as chitin (Seidl 2008). Phosphatase is phosphorus-related enzyme, which is related to mineralization of phosphorus (Schneider et al. 2001). Phosphatase is classified as ACP (orthophosphoric monoester phosphohydrolase, pH 6.5) and ALP (ortho-phosphoric monoester phosphohydrolase, pH 11) according to its optimum pH.

The activities of BG, NAG, ACP, and ALP were determined on the basis of released p-nitrophenol concentration when soils were incubated with p-nitrophenyl (pNP)-linked substrates in a buffer of optimum pH (Verchot and Borelli 2005). In brief, soil slurries for BG, NAG, and ACP activity assays were prepared by mixing 2 g of soil with 40 mL of 50 mM acetate buffer (pH 5.0) using a homogenizer. Soil slurries for ALP activity assays were suspended in 100 mM tris buffer at pH 8.0. Two milliliters aliquots of soil slurry were pipetted into 15 mL conical tube, and 2 mL of 10 mM substrate solution was added to each tube. The substrates used for BG, NAG, ACP, and ALP were pNP-β-D-glucopyranoside, pNP-β-N-acetylglucosaminide, pNP-phosphate (buffer pH 5.0) and pNP-phosphate (buffer pH 8.0), respectively. The tubes were placed on a shaker to be mixed for incubation. Incubation times for assays were as followed: BG and NAG 3 hours, ACP and ALP 2 hours. After incubation, 0.2 mL of 1 N NaOH was added to terminate the reaction and cause color change. Each solution was brought to a final volume of 10 mL using deionized water,

and the tubes were centrifuged at 3000 rpm for 5 minutes. The light absorbance of supernatants were measured at 410 nm. Sample (2 mL buffer + 2 mL soil slurry) and substrate controls (2 mL buffer + 2 mL substrate solution) were conducted during each incubation to control for color development due to the substrate or dissolved humic substances. Final absorbance of each sample was calculated by subtracting the sample control and substrate control absorbance from the sample assay absorbance. All the enzyme activities were expressed as μmol pNP g-dry soil^{-1} h^{-1}.

The stoichiometry of soil enzyme activities was analyzed using the ratio of BG:NAG:(ACP+ALP) activities. Soil C:N:P acquisition ratio measured by the ratio of BG:NAG:(ACP+ALP) activities is the indicator of the relative C, N, and P limitations on microorganisms (Sinsabaugh et al. 2009). Ratios of BG/NAG, BG/(ACP+ALP), and NAG/(ACP+ALP) activities are indicators of microbial demand for C relative to N, C relative to P, and N relative to P, respectively.

2.6 Soil microbial biomass

Microbial biomass was estimated by using a modification of the method of Nunan et al. (1998). In brief, 5 g of soil was weighed in duplicate, and one set of subsamples was fumigated for 24 hours in a desiccator containing 50 mL of chloroform in a beaker. Following fumigation, fumigated subsamples were placed in a fume hood to remove chloroform. The other set of unfumiated subsamples was stored at 4°C. Fumigated and unfumigated soils were extracted with 20 mL of 0.5 M K_2SO_4 solution for 1 hour using a shaker, and filtered through a Whatman no. 42 filter paper. The UV absorbance of fumigated and unfumigated filtrates were measured at 280 nm. Soil microbial biomass was expressed as the increase in absorbance at 280 nm after fumigation on an oven-dried soil basis.

2.7 Data analysis

Importance values were calculated as the average of relative cover and relative density. Species diversity and species richness were calculated with Simpson Index and Menhinick Index, respectively (Simpson 1949, Menhinick 1964). Community classification was conducted using TWINSPAN (Two-way Indicator Species Analysis). The cut levels were selected as 2, 5, 10 and 20. The ordination methods were used to reveal variations in vegetation along the soil physicochemical variable gradient for each period. Since preliminary analysis using detrended correspondence analysis (DCA) suggested a linear response by the species (the length of first axes = 0.55, 0.46, and 0.43 for pre-flooding, post-flooding 1, and post-flooding 2, respectively), a linear model with redundancy analysis (RDA) was carried out in order to analyze the relationship between vegetation and soil physicochemical properties. For this analysis, rare species, which appeared at only one quadrat for each period, were excluded to reduce their influence on the ordination. The Monte Carlo Permutation test (with 999 permutations) was applied to identify the statistical significance of the relationship between them.

Repeated measures ANOVA (rmANOVA) was used to analyze seasonal and spatial variations of soil physicochemical properties (pH, EC, moisture content, organic matter content, concentrations of NO_3-N, NH_4-N, PO_4-P and cations (K^+, Na^+, Ca^{2+}, Mg^{2+}), and contents of sand, silt and clay) with elevation (low, middle and high) as a between-subjects factor and time (pre-flooding, post-flooding 1 and 2) as a within-subject factor. Equality of covariance matrices and sphericity were tested using Box's test and Mauchly's test, respectively. When the assumption of sphericity could not be met, Huynh-Feldt correction was applied to produce a valid *F* ratio (Huynh and Feldt 1976). Since organic matter content did not meet the assumption

of equality of covariance matrices and could not be transformed, these data were analyzed using Friedman's test (a nonparametric analog to rmANOVA). Repeated measures ANOVA was again used to analyze seasonal and spatial variations of soil biological properties such as enzyme activities (BG, NAG, ACP and ALP), microbial biomass, and CO_2 efflux with elevation (low, middle and high) as a between-subjects factor and time (pre-flooding, post-flooding 1 and 2) as a within-subject factor.

The differences in the soil physicochemical properties and soil biological properties among different elevations (low, middle and high) for each period were determined by using one way ANOVA followed by a Duncan or Games-Howell test for equal or unequal variances, respectively. Normality and homogeneity of variance were tested using Shapiro-Wilks test and Levene's test, respectively. Some data that did not meet the normality assumption and could not be transformed were analyzed by Kruskal-Wallis followed by Bonferroni's test.

The relationship between soil biological properties (soil enzyme activities, microbial biomass, and CO_2 efflux) and soil physicochemical properties and vegetation traits was analyzed by Pearson correlation analysis. The ordination methods were used to reveal variations in soil biological properties along the vegetation trait and soil physicochemical variable gradient for each period. Since preliminary analysis using detrended correspondence analysis (DCA) suggested a linear response (the length of first axes = 0.53, 0.57, and 0.49 for pre-flooding, post-flooding1, and post-flooding 2, respectively), a linear model with redundancy analysis (RDA) was used to identify the relationship between soil physicochemical properties and vegetation and variations in soil biological properties. The Monte Carlo Permutation test (with 999 permutations) was applied to identify the statistical significance of the relationship between them.

The rmANOVA was conducted by using SPSS 22.0 for Windows (SPSS Inc., Chicago, IL), and the other statistical analysis were performed using R version 3.6.1 (R Core Team 2018). Significance level was 0.05 for all performed statistical tests.

3. Results

3.1 Soil physicochemical properties

Flooding resulted in great temporal and spatial variations in most of the measured soil physicochemical properties (Table 1). The repeated measures ANOVA (rmANOVA) indicated that seasonal change was significant for nearly all soil physicochemical properties. There were significant differences in moisture content ($F_{2, 27}$ = 74.419, p < 0.001), concentrations of NO_3-N ($F_{2, 27}$ = 5.936, p < 0.01), NH_4-N ($F_{2, 27}$ = 9.126, p < 0.01), PO_4-P ($F_{2, 27}$ = 3.506, p < 0.05), K^+ ($F_{2, 27}$ = 7.013, p < 0.01), and Na^+ ($F_{2, 27}$ = 43.993, p < 0.001) among different elevations. The rmANOVA results showed that the interaction between elevation and seasonal change was significant only for moisture content ($F_{4, 54}$ = 6.726, p < 0.001) and NO_3-N concentration ($F_{3.12, 54}$ = 4.310, p < 0.01). There was a clear effect of elevation over time on organic matter content (Friedman χ^2 = 16.067, p < 0.001).

Table 1. The effects of elevation and time on soil physicochemical properties based on repeated measures ANOVA (rmANOVA) or Friedman's test.

Test	Measured variable	Model	df	Test statistic (F value or χ^2)	p
rmANOVA	pH	Elevation	2, 27	0.562	ns
		Time	2, 54	8.516	**
		Elevation × Time	4, 54	1.117	ns
	EC	Elevation	2, 27	0.457	ns
		Time	1.52, 54	53.093	***
		Elevation × Time	3.04, 54	0.713	ns
	Moisture content	Elevation	2, 27	74.419	***
		Time	2, 54	10.270	***
		Elevation × Time	4, 54	6.726	***
	NO_3-N	Elevation	2, 27	5.936	**
		Time	1.56, 54	1.165	ns
		Elevation × Time	3.12, 54	4.310	**
	NH_4-N	Elevation	2, 27	9.126	**
		Time	2, 54	88.540	***
		Elevation × Time	4, 54	0.555	ns
	PO_4-P	Elevation	2, 27	3.506	*
		Time	1.72, 54	40.030	***
		Elevation × Time	3.43, 54	1.115	ns
	K^+	Elevation	2, 27	7.013	**
		Time	1.79, 54	4.100	*
		Elevation × Time	3.58, 54	0.125	ns
	Na^+	Elevation	2, 27	43.993	***
		Time	2, 54	16.964	***
		Elevation × Time	4, 54	1.946	ns
	Ca^{2+}	Elevation	2, 27	1.097	ns
		Time	2, 54	2.674	ns
		Elevation × Time	4, 54	1.681	ns
	Mg^{2+}	Elevation	2, 27	1.964	ns
		Time	2, 54	12.780	***
		Elevation × Time	4, 54	1.388	ns
	Sand	Elevation	2, 27	1.491	ns
		Time	2, 54	15.672	***
		Elevation × Time	4, 54	0.793	ns
	Silt	Elevation	2, 27	2.409	ns
		Time	2, 54	13.552	***
		Elevation × Time	4, 54	2.257	ns
	Clay	Elevation	2, 27	1.004	ns
		Time	2, 54	95.465	***
		Elevation × Time	4, 54	0.165	ns
Friedman's test	Organic matter content	Nonparametric	2	16.067	***

Test statistics for rmANOVA and Friedman's test were F value and χ^2, respectively.
ns indicates no significance ($p > 0.05$).
Significance level at $p < 0.05$, *; $p < 0.01$, **; $p < 0.001$, ***

Moisture content differed significantly among different elevations. Moisture content showed a decreasing trend with higher elevation in both pre- and post-flooding (Table 2). Organic matter content of high elevation was significantly lower than that of the other elevations in both pre- and post-flooding. Although soil pH and EC remarkably increased after flooding, no significant difference was found among different elevations. Regarding soil particle distribution, prior to flooding, the sand content of high elevation was significantly higher than that of the other elevations, whereas the opposite pattern was observed for the silt content. After flooding, overall content of sand increased, while overall content of silt and clay decreased. There was no significant spatial variation in soil particle distribution after flooding. In terms of nutrient availability, NO_3-N concentration decreased and NH_4-N concentration increased in post-flooding 1. In pre-flooding and post-flooding 1, NH_4-N concentration was significantly higher in low elevation than that of the other elevations, whereas in post-flooding 2, there was no significant difference among elevations due to an overall increase in NH_4-N concentration. No significant difference in PO_4-P concentration was found among elevations, and PO_4-P concentration decreased remarkably after flooding. In the case of cation contents, K^+ concentration showed an increasing trend with higher elevation, whereas the opposite trend was observed for Na^+ concentration. Although Ca^{2+} concentration ranged from 286.33 to 1584.78 mg/kg in the study sites during the study period, no significant temporal or spatial variations were observed. There was no significant difference in Mg^{2+} concentration among different elevations, and the overall concentration of Mg^{2+} was lower in post-flooding 2.

Table 2. Variations of soil physicochemical properties under different elevations during the study period (mean±SE).

	Pre-flooding			Post-flooding 1			Post-flooding 2		
	Low	Middle	High	Low	Middle	High	Low	Middle	High
pH	4.90±0.22a	5.14±0.15a	4.80±0.13a	5.28±0.18a	5.30±0.11a	5.23±0.11a	5.03±0.18a	5.18±0.11a	5.14±0.11a
EC (μS/cm)	11.72±1.07b	14.01±1.01ab	16.08±0.98a	37.67±3.98a	36.14±4.49a	34.43±3.20a	31.36±2.57a	31.61±2.23a	35.76±1.79a
Moisture content (%)	52.67±0.84a	46.85±1.52b	29.66±1.59c	50.33±2.66a	37.74±1.91b	28.25±1.03c	47.87±1.73a	45.20±1.33a	32.60±0.81b
Organic matter content (%)	9.91±0.22a	10.99±0.55a	8.02±0.43b	10.23±0.89a	8.72±0.65ab	6.59±0.24b	8.93±0.96ab	10.15±0.56a	7.36±0.29b
NO_3-N (mg/kg)	1.64±0.23a	1.91±0.21a	1.82±0.18a	1.36±0.24a	1.66±0.22a	1.53±0.12a	1.12±0.08b	1.49±0.29b	2.82±0.34a
NH_4-N (mg/kg)	8.59±2.54a	3.98±1.40b	2.35±0.51b	13.68±2.69a	6.28±1.00b	4.76±0.73b	45.14±8.56a	37.93±6.15a	29.60±4.05a
PO_4-P (mg/kg)	23.40±7.87a	14.34±2.21a	11.65±2.29a	6.90±1.28a	4.68±0.35ab	4.09±0.32b	4.59±0.39a	4.71±0.45a	5.07±0.45a
K^+ (mg/kg)	122.30±23.21a	149.28±27.91a	207.51±23.57a	166.06±29.96b	172.38±7.70b	253.95±24.92a	106.73±31.41a	125.23±30.57a	177.95±24.13a
Na^+ (mg/kg)	47.35±4.11a	55.84±3.76a	22.04±2.62b	44.04±6.93a	39.19±6.70a	10.32±1.01b	35.51±4.21a	36.11±4.17a	12.78±2.01b
Ca^{2+} (mg/kg)	1004.35±65.85a	1184.78±84.04a	970.30±64.28a	980.07±188.44a	1234.95±84.92a	1082.94±76.17a	930.29±99.97a	962.87±87.12a	1023.22±68.32a
Mg^{2+} (mg/kg)	265.04±29.15a	328.58±24.36a	300.11±15.57a	217.37±46.43a	303.25±24.63a	295.15±18.92a	199.79±18.30a	208.09±18.54a	244.58±25.08a
Sand (%)	25.55±2.91b	24.14±1.18b	29.53±2.55a	30.40±4.05a	31.31±2.73a	32.97±2.28a	41.13±5.29a	33.38±2.06a	39.59±2.84a
Silt (%)	68.41±1.19a	64.96±1.24ab	59.15±1.55b	60.84±1.98a	62.76±2.29a	60.73±2.05a	53.40±4.72a	60.00±1.82a	54.17±2.43a
Clay (%)	9.71±0.92a	10.86±0.85a	9.96±0.51a	6.24±1.08a	7.06±0.56a	6.17±0.71a	5.47±0.67a	6.62±0.48a	5.29±0.50a

Letters indicate significant differences among elevations in each period (a>b>c).

3.2 Vegetation

Significant differences in aboveground biomass and species diversity existed among periods. Aboveground biomass ranged from 10.7 to 64.5 g/0.09 m^2 in pre-flooding, and showed an increasing trend with higher elevation ($R^2 = 0.583$, $p < 0.001$; Figure 5a). In contrast, the relationship between elevation and above-ground biomass showed a U-shaped distribution in both post-flooding 1 ($R^2 = 0.199$, $p = 0.050$) and post-flooding 2 ($R^2 = 0.433$, $p < 0.001$). In post-flooding 1, aboveground biomass varied widely from 17.4 to 135.9 g/0.09 m^2, and was significantly higher than that of the other two periods (Figure 5b). In post-flooding 2, aboveground biomass was lower than post-flooding 1 with ranges of 20.0 to 120.7 g/0.09 m^2 (Figure 5c).

On the other hand, the relationship between elevation and species diversity showed a skewed unimodal pattern with the largest index occurring at the middle elevation of 60-80 cm in both pre-flooding ($R^2 = 0.233$, $p < 0.05$; Figure 5d) and post-flooding 1($R^2 = 0.246$, $p < 0.05$; Figure 5e). However, there was no significant relationship between elevation and species diversity in post-flooding 2 (Figure 5f).

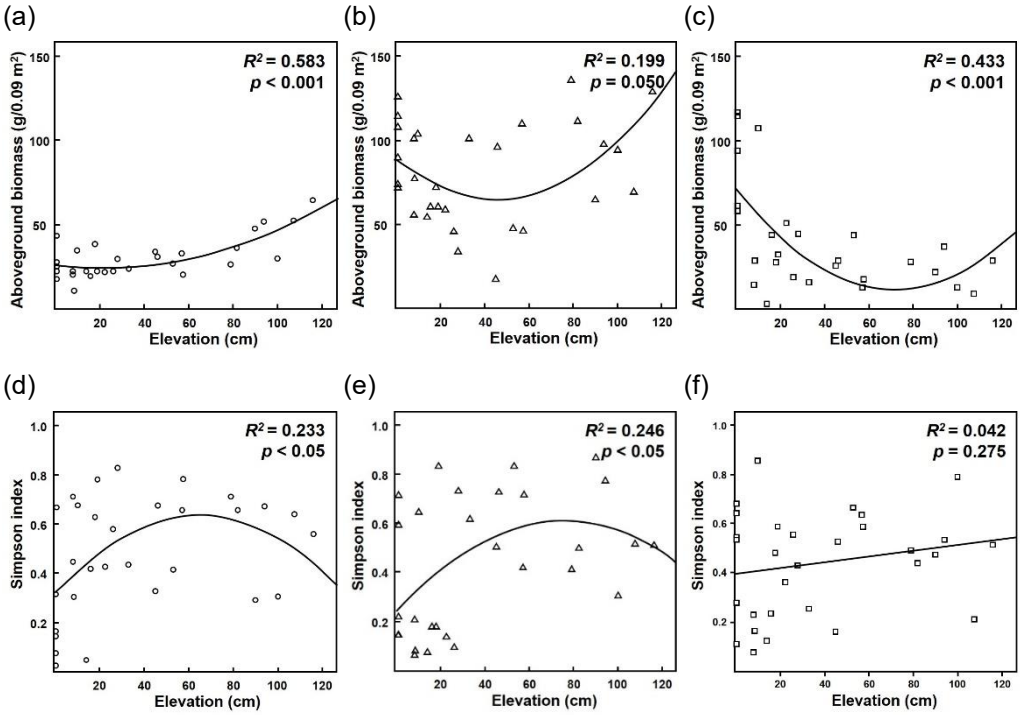


Figure 5. Distribution patterns of aboveground biomass (a, b, c) and species diversity (d, e, f) along a gradient of elevation. (a) and (d), pre-flooding; (b) and (e), post-flooding 1; (c) and (f), post-flooding 2. Solid lines are trend lines.

There was an obvious temporal variation in species composition (Table 3, Figure 6). *Zizania latifolia*, *Polygonum thunbergii, Phragmites australis* were dominant throughout the field survey periods. Prior to flooding, *Artemisia vulgaris*, *Phalaris arundinacea*, *Miscanthus sacchariflorus,* and *Galium spurium* were dominant, while *M. sacchariflorus* was widely distributed until post-flooding 1. *Bidens frondosa*, *Artemisia princeps,* and *Humulus scandens* began to grow late and dominated after flooding. In post-flooding 2, *A. princeps* were dominant, and *Stellaria aquatica* displaced *P. australis*.

There were significant spatial variations in species composition and distribution patterns (Table 3, Figure 6). Spatial difference showed a clear relationship with the elevation above the water level. At low elevation, which is permanently flooded, dominant species did not change significantly over period. *Zizania latifolia*, an obligate wetland plant, was constantly dominant in both pre- and post-flooding, and *B. frondosa* was also found at low elevation after flooding. Prior to flooding, *P. thunbergii* and *A. vulgaris* were dominant within a range of elevations of 8-26 cm and 26-45 cm, respectively, which are periodically flooded. *Phragmites australis*, which is an obligate wetland plant, was widely distributed at elevations of 57-110 cm. Species composition and distribution patterns have changed after flooding. In post-flooding 1, *P. thunbergii* was dominant at middle elevation with most other species decreasing. *Phragmites australis* was widely distributed at high elevation. Invasive or pioneer plants, including *A. princeps*, *H. scandens,* and *Sicyos angulatus*, were observed above the elevation of 28 cm. In post-flooding 2, *P. thunbergii* was still distributed over a wide range of periodically flooded areas. Obligate upland plants including *A. princeps* and *H. scandens* were widely distributed above the elevation of 19 cm, and *P. australis* was dominant above the elevation of 28 cm.

Table 3. Species list in the studied riparian zone.

Species	Frequency	Degree of wetness	Pre-flooding			Post-flooding 1			Post-flooding 2		
			L	M	H	L	M	H	L	M	H
Achyranthes bidentata Blume	OBU									O	
Actinostemma lobatum (Maxim.) Maxim. ex Franch. & Sav.	FAC		O	O	O	O	O	O	O	O	
Alopecurus aequalis Sobol.	FACW	HYG		O							
Artemisia vulgaris L.	FACW	HYG		O	O			O			
Artemisia princeps Pamp.	OBU						O	O		O	O
Beckmannia syzigachne (Steud.) Fernald	FAC			O							
Bidens frondosa L.	FACW	HYG	O			O	O	O	O	O	
Calystegia hederacea Wall.	OBU				O						
Chelidonium asiaticum (Hara) Krahulc.	OBU										O
Commelina communis L.	OBU						O	O			
Corydalis pauciovulata Ohwi	OBU									O	O
Eclipta prostrata (L.) L.	FACW	HYG				O					
Equisetum arvense L.	FACU			O	O			O		O	O
Erechtites hieracifolia (L.) Raf.	OBU						O				
Festuca parvigluma Steud.	OBU			O							
Galium spurium L.	OBU			O	O						
Glycine max subsp. *soja* (Siebold & Zucc.) H.Ohashi	OBU			O	O		O	O		O	O
Humulus scandens (Lour.) Merr.	OBU		O	O	O		O	O		O	O
Isachne globosa (Thunb.) Kuntze	OBW	HYG							O		
Ixeris polycephala Cass.	FACU			O							
Lactuca indica L.	OBU							O			
Lamiaceae a					O						
Ludwigia prostrata Roxb.	OBW	HYG				O			O	O	O
Menispermum dauricum DC.	OBU				O						
Miscanthus sacchariflorus (Maxim.) Hack.	FACW	HYG		O	O		O	O		O	O

Mosla dianthera (Buch.-Ham. ex Roxb.) Maxim.	OBU							O			O
Oenanthe javanica (Blume) DC.	OBW	EMER	O		O					O	
Panicum bisulcatum Thunb.	FAC										O
Persicaria longiseta (Bruijn) Kitag.	OBU								O		
Phalaris arundinacea L.	FACW	HYG		O	O		O				
Phragmites australis (Cav.) Trin. ex Steud.	OBW	EMER	O	O	O	O	O	O	O	O	O
Polygonum lapathifolium var. lapathifolium	OBU			O		O		O	O	O	O
Polygonum thunbergii Siebold & Zucc.	FACW	HYG	O	O	O	O	O	O	O	O	O
Polygonum perfoliatum L.	OBU		O	O	O			O			
Rorippa indica (L.) Hiern	FAC		O								
Rorippa palustris (L.) Besser	FAC		O	O							
Rubiaceae a											O
Rumex crispus L.	FAC			O	O				O		O
Sagittaria aginashii Makino	OBW	EMER				O					
Salix gracilistyla Miq.	FACW	HYG			O			O			
Salix triandra L.	FACW	HYG			O			O			O
Schoenoplectus tabernaemontani (C.C.Gmel.) Palla	OBW	EMER		O			O			O	
Scirpus radicans Schkuhr	OBW	EMER	O	O	O	O	O		O	O	O
Sicyos angulatus L.	FAC						O	O	O	O	O
Stellaria aquatica (L.) Scop.	FAC				O			O			O
Symphyotrichum pilosum (Willd.) G.L.Nesom	OBU							O			O
Triadenum japonicum (Blume) Makino	OBW	HYG									O
Trigonotis peduncularis (Trevir.) Steven ex Palib.	OBU				O						
Veronica undulata Wall.	OBW	HYG	O	O							
Zizania latifolia (Griseb.) Turcz. ex Stapf	OBW	EMER	O	O	O	O	O		O	O	

L: low; M: middle; H: high; OBU: obligate upland plant; FACU: facultative upland plant; FAC: facultative plant; FACW: facultative wetland plant; OBW: obligate wetland plant; HYG: hygrophyte; EMER: emergent

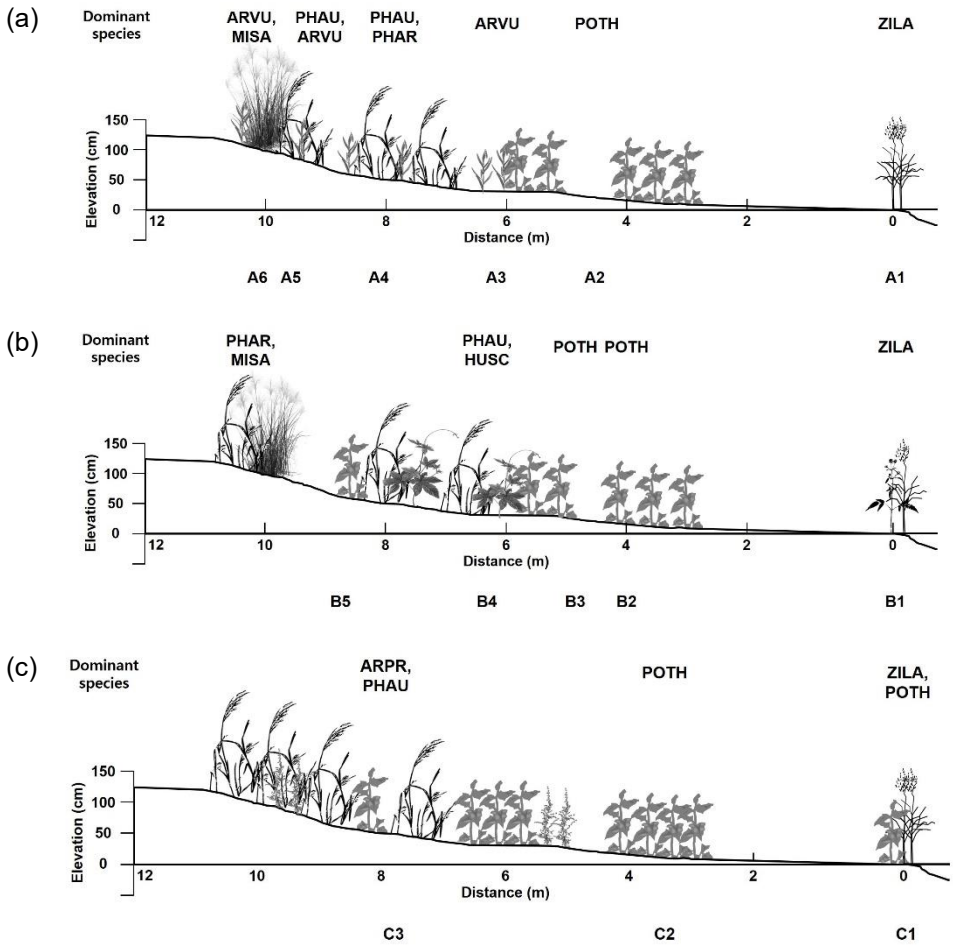


Figure 6. Systematic diagram of bisect and dominant species in pre-flooding (a), post-flooding 1 (b), and post-flooding 2 (c). ARPR: *Artemisia princeps*; ARVU: *Artemisia vulgaris;* HUSC: *Humulus scandens;* PHAR: *Phalaris arundinacea;* PHAU: *Phragmites australis;* POTH: *Polygonum thunbergii;* MISA: *Miscanthus sacchariflorus;* ZILA: *Zizania latifolia.*

3.3 Relationship between vegetation and soil physico-chemical properties

TWINSPAN classified 30 quadrats of pre-flooding, post-flooding 1 and 2 into 6 (labeled A1-A6), 5 (labeled B1-B5), and 3 groups (labeled C1-C3), respectively (Figure 7). A1 includes 6 quadrats dominated by *Z. latifolia,* and was located at low elevation. Seven quadrats of A2 were dominated by *P. thunbergii,* and were located at middle elevation. *Artemisia vulgaris* was a common species at A3, A4, A5, and A6, which were located at high elevation. A3 comprises 5 quadrats dominated by *A. vulgaris*. A4 includes 2 quadrats, where *P. australis, P. arundinacea,* and *A. vulgaris* were common species. Eight quadrats of A5 were closely related to *A. vulgaris, P. australis,* and *G. spurium*. A6 includes 2 quadrats, where *A. vulgaris* and *M. sacchariflorus* were common species.

After flooding, classification of vegetation changed. B1 includes 6 quadrats which were located at low elevation, where *Z. latifolia* and *B. frondosa* were common species. B2 and B3 comprise 1 and 10 quadrats, respectively, dominated by *P. thunbergii,* and most of them were located at middle elevation. B4 includes 9 quadrats dominated by *P. australis* and *H. scandens.* Four quadrats of B5 were closely related to *P. australis* and *M. sacchariflorus.* The most common species in C1, including 8 quadrats, were *Zizania latifolia*, *B. frondosa,* and *P. thunbergii.* Eleven quadrats of C2 were dominated by *P. thunbergii,* where *H. scandens* was a common species. C3 includes 11 quadrats, where *P. australis* and *A. princeps* were common species.

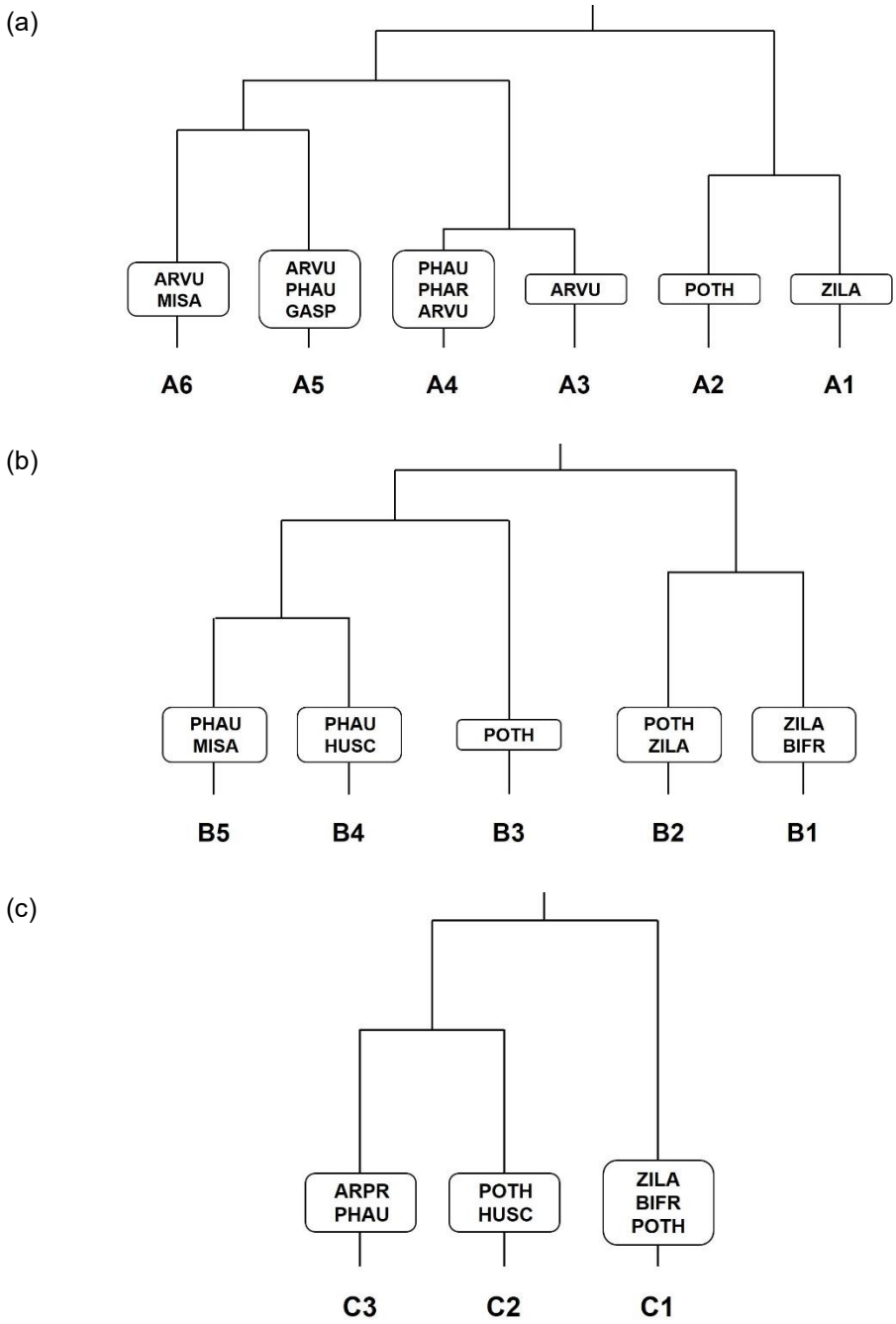


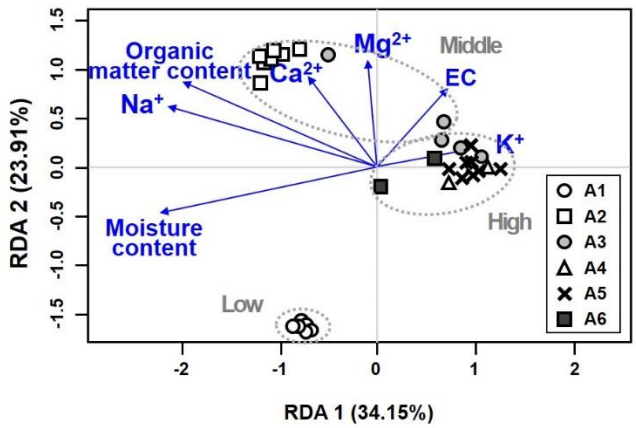
Figure 7. TWINSPAN dendrogram of pre-flooding (a), post-flooding 1 (b), and post-flooding 2 (c) with indicator species for each group. ARPR: *Artemisia princeps*; ARVU: *Artemisia vulgaris;* BIFR: *Bidens frondosa;* GASP: *Galium spurium;* HUSC: *Humulus scandens;* PHAR: *Phalaris arundinacea;* PHAU: *Phragmites australis;* POTH: *Polygonum thunbergii;* MISA: *Miscanthus sacchariflorus;* ZILA: *Zizania latifolia.*

The Redundancy analysis (RDA) ordination displayed scores for all of the quadrats with the arrows indicating the relative directions and strengths of the soil physicochemical variable gradient (Figure 8). When plotted on the RDA ordination axes, the quadrats tended to be separated into the vegetation community resulted from TWINSPAN. The quadrats were also clearly separated according to the elevation (low, middle, and high). The first two axes explained 58.06%, 52.84%, and 47.79% of the variance in pre-flooding, post-flooding 1, and post-flooding 2, respectively.

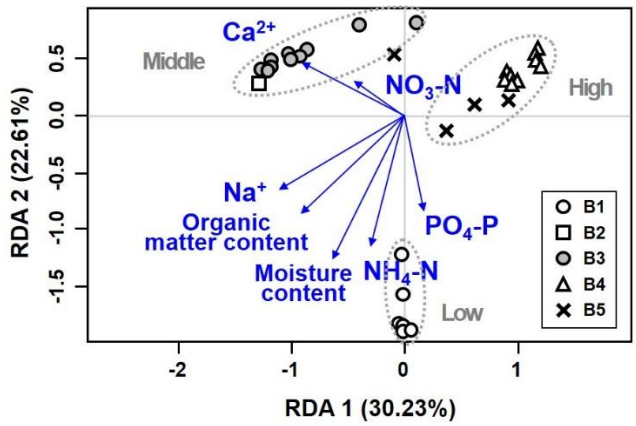
Prior to flooding, moisture content was the most principal factor, explaining 18.75% of the variation of vegetation ($p < 0.001$). Furthermore, organic matter content ($F = 10.35$, $p < 0.001$), EC ($F = 5.14$, $p < 0.001$), Ca^{2+} ($F = 4.75$, $p < 0.01$), K^{+} ($F = 4.71$, $p < 0.01$), Mg^{2+} ($F = 3.74$, $p < 0.01$), and Na^{+} concentrations ($F = 3.10$, $p < 0.05$) could significantly explain the variation.

After flooding, main factors responsible for the variation of vegetation changed. The RDA of post-flooding 1 indicated that moisture content was still the principal factor ($F = 12.15$, $p < 0.001$). Organic matter content ($F = 4.19$, $p < 0.001$), Na^{+} ($F = 4.63$, $p < 0.01$), NO_3-N ($F = 2.97$, $p < 0.05$), PO_4-P ($F = 2.82$, $p < 0.05$), Ca^{2+} ($F = 2.48$, $p < 0.05$), and NH_4-N concentrations ($F = 2.43$, $p < 0.05$) could significantly explain the variation. The RDA of post-flooding 2 revealed that moisture content ($F = 9.56$, $p < 0.001$), organic matter content ($F = 8.06$, $p < 0.001$), pH ($F = 2.58$, $p < 0.05$), and EC ($F = 2.36$, $p < 0.05$) were principal factors.

(a)



(b)



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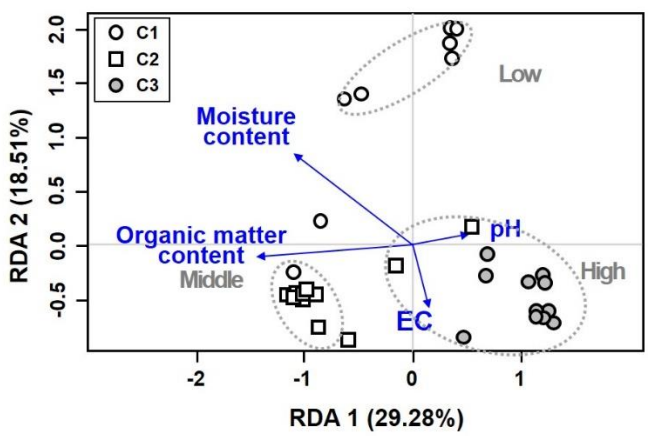

Figure 8. Redundancy analysis (RDA) ordination of vegetation quadrats (*n* = 30) and soil physicochemical variables (arrows) for pre-flooding (a), post-flooding 1 (b), and post-flooding 2 (c).

3.4 Soil biological properties

Flooding resulted in great temporal and spatial variations in most of the measured soil enzyme activities, but not in CO_2 efflux (Table 4). There was a significant difference in NAG ($F_{2, 27}$ = 36.092, p < 0.001), ACP ($F_{2, 27}$ = 8.904, p < 0.01), and ALP activities ($F_{2, 27}$ = 5.832, p < 0.01) among different elevations. Seasonal change was significant for ACP ($F_{1.75, 54}$ = 1.750, p < 0.001) and ALP activities ($F_{1.58, 54}$ = 62.392, p < 0.001). The rmANOVA showed that the interaction between elevation and seasonal change was significant for NAG ($F_{4, 54}$ = 3.895, p < 0.05), ACP ($F_{3.50, 54}$ = 3.500, p < 0.05), and ALP activities ($F_{3.17, 54}$ = 3.725, p < 0.05). There was a clear effect of elevation over time on BG activity (Friedman χ^2 = 22.400, p < 0.001), and there was a temporal variation in microbial biomass (Friedman χ^2 = 40.067, p < 0.001).

Table 4. The effects of elevation and time on soil biological properties based on repeated measures ANOVA (rmANOVA) or Friedman's tests.

Test	Measured variable		Model	df	Test statistic (F value or χ^2)	p
rmANOVA	Soil enzyme activity	NAG	Elevation	2, 27	36.092	***
			Time	2, 54	3.079	ns
			Elevation × Time	4, 54	3.895	**
		ACP	Elevation	2, 27	8.904	**
			Time	1.75, 54	1.750	***
			Elevation × Time	3.50, 54	3.500	*
		ALP	Elevation	2, 27	5.832	**
			Time	1.58, 54	62.392	***
			Elevation × Time	3.17, 54	3.725	*
	CO_2 efflux		Elevation	2, 27	1.232	ns
			Time	1.79, 54	0.529	ns
			Elevation × Time	3.57, 54	0.072	ns
Friedman's test	Soil enzyme activity	BG	Nonparametric	2	22.400	***
	Microbial biomass		Nonparametric	2	40.067	***

Test statistics for rmANOVA and Friedman's test were F value and χ^2, respectively.
ns indicates no significance ($p > 0.05$).
Significance level at $p < 0.05$, *; $p < 0.01$, **; $p < 0.001$, ***

Individual enzyme activity responded differently to seasonal change and different elevations. Prior to flooding, BG and NAG activities showed decreasing trends with higher elevation. This decreasing trend continued for BG activity after flooding, while overall BG activity decreased in post-flooding 2 (Figure 9a). NAG activity at low elevation was significantly higher than that of the other elevations in pre-flooding and post-flooding 1, whereas no significant spatial variation was observed due to a decrease in NAG activity at low elevation in post-flooding 2 (Figure 9b). Prior to flooding, ACP activity showed a decreasing trend with higher elevation despite the lack of statistical significance. After flooding, ACP activity at low elevation increased in post-flooding 1, whereas it decreased again in post-flooding 2 resulting in no significant difference among elevations (Figure 9c). Prior to flooding, ALP activity was the highest at middle elevation. After flooding, there was a decreasing trend with higher elevation in post-flooding 1, whereas there was no significant difference in ALP activity among elevations in post-flooding 2 due to an overall decrease (Figure 9d).

There were no significant differences in microbial biomass among different elevations (Figure 9e). Although CO_2 efflux of middle elevation was higher than that of the other elevations during the survey period, it was not statistically significant difference (Figure 9f).

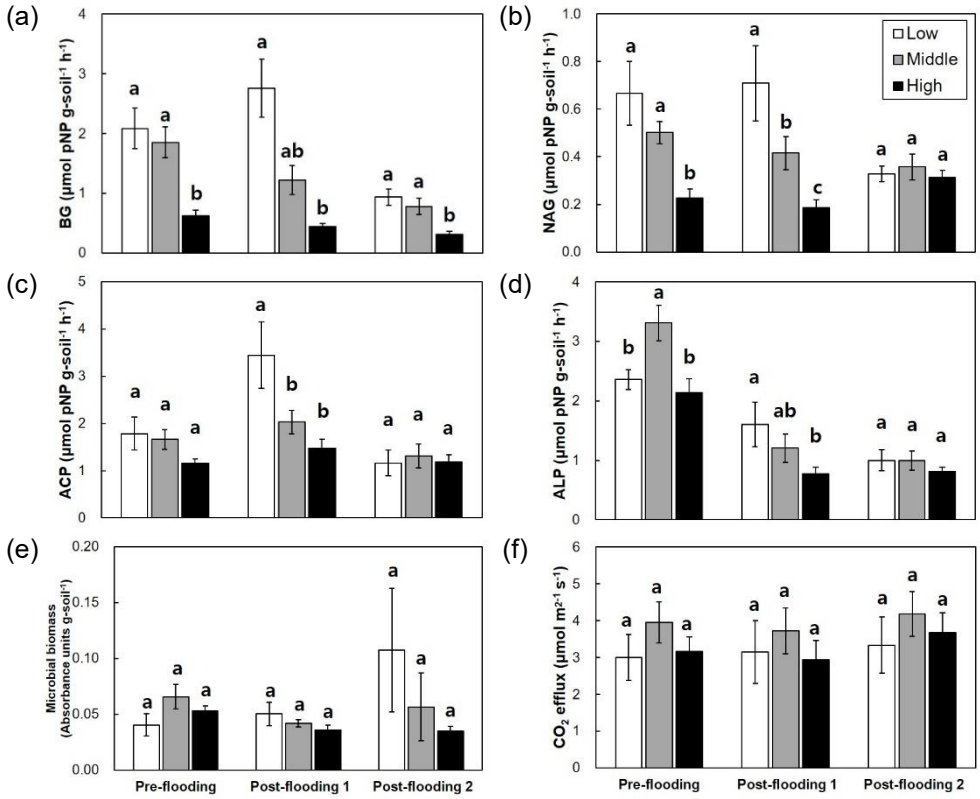

Figure 9. Variations of soil biological properties under different elevations during the study period (mean±SE). Letters indicate significant differences among elevations in each period (a>b>c).

The stoichiometry of BG, NAG, ACP, and ALP activities was analyzed. BG/NAG ratios were >1, whereas BG/(ACP+ALP) ratios were <1 for all elevations during the survey period (Figure 10). In addition, NAG/(ACP+ALP) ratios were all <1 for all elevations during the survey period, varied from 0.02 to 0.40 (not shown as data).

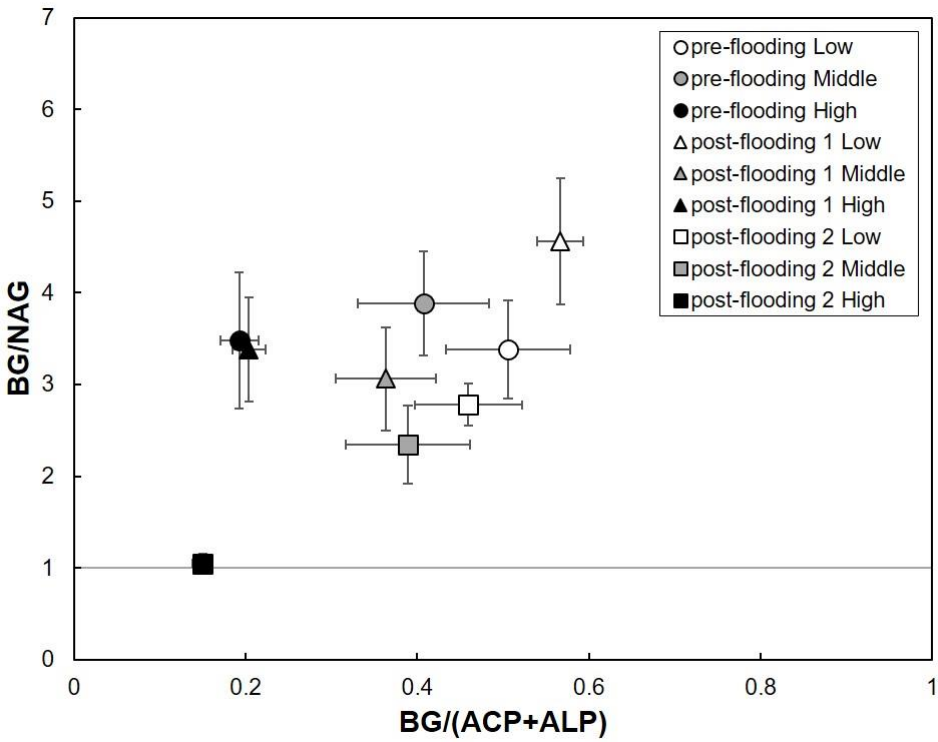

Figure 10. The stoichiometry of soil enzyme activities under different elevations during the study period (mean±SE).

3.5 Relationship between soil biological properties and soil physicochemical properties and vegetation

The redundancy analysis (RDA) showed the relative contributions of soil physicochemical properties or vegetation traits to soil biological properties including soil enzyme activities, microbial biomass, and CO_2 efflux (Figure 11). The RDA indicated that the first two axes explained 52.32%, 56.11%, and 28.19% of the variance of soil biological properties in pre-flooding, post-flooding 1, and post-flooding 2, respectively. Prior to flooding, moisture content was the most principal factor explaining the variation of soil biological properties (F = 17.10, p < 0.001). Furthermore, organic matter content (F = 14.10, p < 0.001), PO_4-P concentration (F = 3.45, p < 0.05), and pH (F = 2.86, p < 0.05) could significantly explain the variation.

After flooding, main factors responsible for the variation of soil biological properties changed. The RDA of post-flooding 1 indicated that moisture content was still the most principal factor explaining the variation (F = 28.74, p < 0.001), and pH could also significantly explain the variation (F = 5.77, p < 0.01). The RDA of post-flooding 2 showed that PO_4-P concentration (F = 4.37, p < 0.01), organic matter content (F = 3.42, p < 0.05), and aboveground biomass (F = 2.79, p < 0.05) were principal factors explaining the variation.

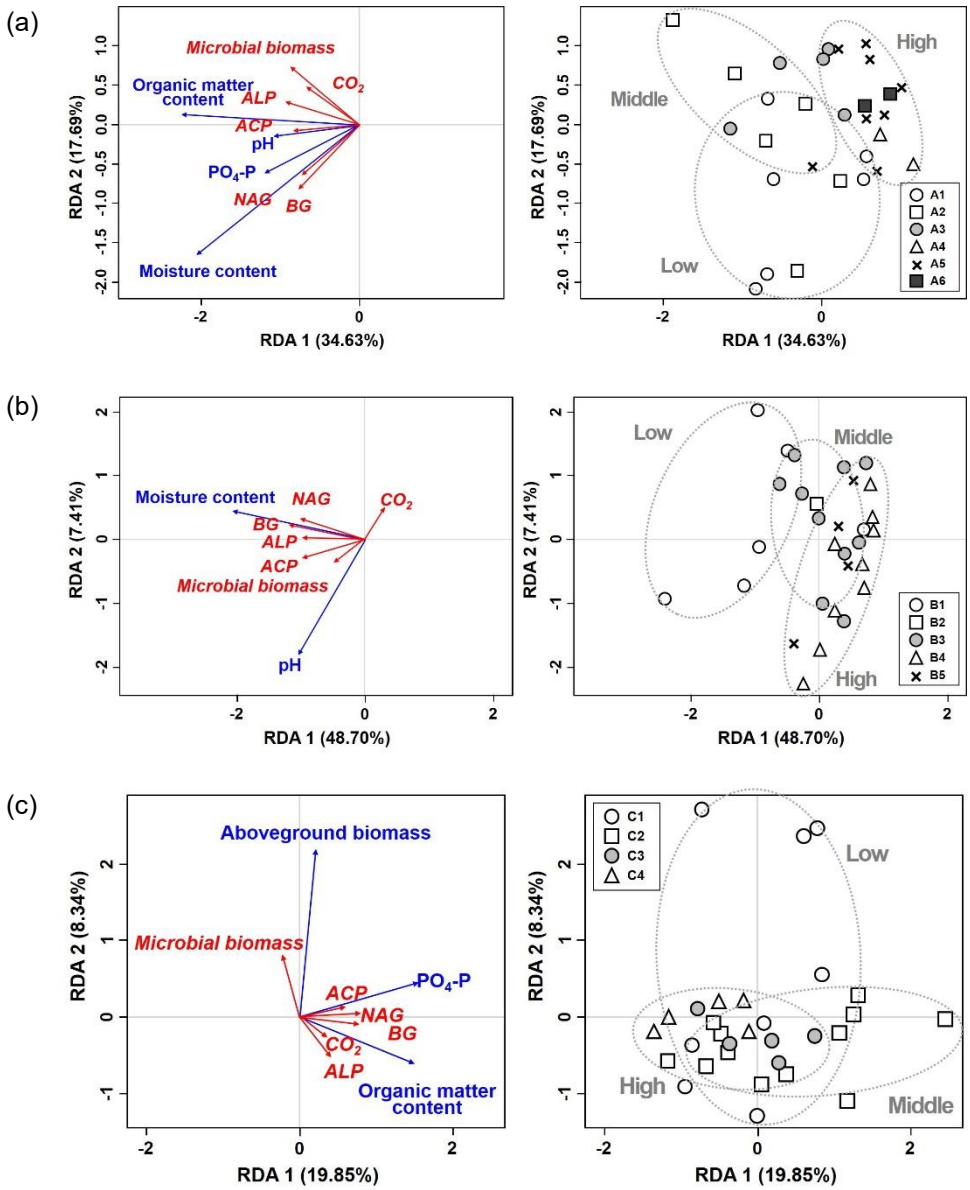

Figure 11. Redundancy analysis (RDA) of soil biological properties (soil enzyme activities, microbial biomass, and CO_2 efflux) and soil physicochemical properties and vegetation in pre-flooding (a), post-flooding 1 (b), and post-flooding 2 (c).

Correlation analysis showed that soil enzyme activities of each period were significantly correlated with several soil physicochemical properties and vegetation traits, and flooding had an effect on the relationships between them (Table 5).

Prior to flooding, pH, moisture content, organic matter content, NH_4-N, PO_4-P, cation (K^+, Na^+, Ca^{2+}, Mg^{2+}) concentrations, and soil particle distribution significantly impacted soil enzyme activities. Moisture content was significantly correlated with all measured enzyme activities (r = 0.821, 0.730, 0.478, and 0.430 for BG, NAG, ACP, and ALP activities, respectively). BG activity was positively correlated to moisture content, organic matter content, NH_4-N and Na^+ concentrations, and silt content. BG activity showed negative correlation with K^+ concentration, sand content, and aboveground biomass. In the case of NAG activity, it was positively correlated to moisture content, organic matter content, NH_4-N, PO_4-P, and Na^+ concentrations, and silt content, whereas it was negatively correlated to K^+ concentration and sand content. Significantly positive correlations were observed between ACP activity and pH, moisture content, PO_4-P and Na^+ concentrations. ALP activity showed significantly positive correlations with moisture content, organic matter content, Na^+, Ca^{2+}, and Mg^{2+} concentrations, and contents of silt and clay. ALP activity was negatively correlated to sand content. In addition, both ACP and ALP activities were positively correlated to microbial biomass and CO_2 efflux.

Correlation analysis of post-flooding 1 showed that moisture content, organic matter content, NH_4-N, PO_4-P, and Na^+ concentrations were strongly correlated with all measured soil enzyme activities. pH was positively correlated to ACP and ALP activities. Among soil biological properties, microbial biomass was positively correlated to NAG and ACP activities.

Post-flooding 2 correlation analysis showed that BG activity was positively

correlated to moisture content, organic matter content, and Na^+ concentrations. BG activity was negatively correlated to NO_3-N concentration and Simpson index. NAG activity was positively correlated with PO_4-P concentration and negatively correlated with NH_4-N concentration. ACP activity was positively correlated to organic matter content and PO_4-P concentration and negatively correlated to NH_4-N concentration. ALP activity was positively correlated to pH, moisture content, and organic matter content and negatively correlated to EC and PO_4-P concentration.

The results of correlation analysis showed that microbial biomass and CO_2 efflux were significantly correlated with several soil physicochemical properties and vegetation traits. Prior to flooding, microbial biomass was positively correlated to organic matter content, Ca^{2+} and Mg^{2+} concentrations, and sand content. CO_2 efflux showed significantly positive correlations with organic matter content and Ca^{2+} concentration, whereas it was negatively correlated to Menhinick index. Significant positive correlations were observed between microbial biomass and CO_2 efflux. After flooding, the relationships between microbial biomass or CO_2 efflux and several other factors changed. In post-flooding 1, microbial biomass showed positive correlations with pH and moisture content, and CO_2 efflux showed significantly negative correlations with pH and Menhinick index. Contrary to pre-flooding, significantly negative correlations were observed between microbial biomass and CO_2 efflux in post-flooding 1. In post-flooding 2, microbial biomass was positively correlated to aboveground biomass and Menhinick index, while CO_2 efflux was positively correlated to Ca^{2+} concentration and sand content.

Table 5. Correlation coefficients between soil biological properties and soil physicochemical properties and vegetation.

		Pre-flooding						Post-flooding 1						Post-flooding 2					
		BG	NAG	ACP	ALP	MB	CO_2	BG	NAG	ACP	ALP	MB	CO_2	BG	NAG	ACP	ALP	MB	CO_2
Soil physico-chemical properties	pH	ns	ns	**0.49****	ns	ns	ns	ns	ns	**0.57*****	**0.38***	**0.49****	**-0.51****	ns	ns	ns	**0.41***	ns	ns
	EC	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	**-0.37***	ns	ns
	MC	**0.82*****	**0.73*****	**0.48****	**0.43***	ns	ns	**0.93*****	**0.86*****	**0.75*****	**0.69*****	**0.38***	ns	**0.77*****	ns	ns	**0.38***	ns	ns
	OMC	**0.58*****	**0.40**	ns	**0.77****	**0.40***	**0.47****	**0.86*****	**0.81*****	**0.55****	**0.60*****	ns	ns	**0.71*****	ns	**0.38***	**0.38***	ns	ns
	NO_3-N	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	**-0.40***	ns	ns	ns	ns	ns
	NH_4-N	**0.43***	**0.50****	ns	ns	ns	ns	**0.85*****	**0.74*****	**0.62*****	**0.57*****	ns	ns	ns	**-0.36***	**-0.54****	ns	ns	ns
	PO_4-P	ns	**0.50**	**0.52****	ns	ns	ns	**0.55****	**0.47****	**0.57****	**0.57*****	ns	ns	ns	**0.48****	**0.47****	**-0.38***	ns	ns
	K^+	**-0.39***	**-0.42**	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
	Na^+	**0.60*****	**0.57****	**0.39***	**0.57****	ns	ns	**0.73*****	**0.64*****	**0.48****	**0.63*****	ns	ns	**0.61*****	ns	ns	ns	ns	ns
	Ca^{2+}	ns	ns	ns	**0.84*****	**0.51****	**0.42***	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	**0.39***
	Mg^{2+}	ns	ns	ns	**0.61*****	**0.42***	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
	Sand	**-0.40***	**-0.37***	ns	**-0.66*****	**0.51****	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	**0.41***
	Silt	**0.49***	**0.46***	ns	**0.62*****	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
	Clay	ns	ns	ns	**0.58*****	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Vegetation traits	AGBM	**-0.48****	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	**0.62*****	ns
	R	ns	ns	ns	ns	ns	**-0.40***	ns	ns	ns	ns	ns	**-0.47****	ns	ns	ns	ns	**0.50****	ns
	D	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	**-0.44***	ns	ns	ns	ns	ns
Soil biological properties	MB	ns	ns	**0.38***	**0.41***	-	**0.58*****	ns	**0.42***	**0.50****	ns	-	**-0.42***	ns	ns	ns	ns	-	ns
	CO_2	ns	ns	**0.38***	**0.40***	**0.58*****	-	ns	ns	ns	ns	**-0.42***	-	ns	ns	ns	ns	ns	-

BG : β-glucosidase; NAG : β-N-acetylglucosaminidase; ACP : acid phosphatase; ALP : alkaline phosphatase; MC : moisture content; OMC : organic matter content; AGBM : aboveground biomass; R : Menhinick Index; D : Simpson Index
ns indicates no significant linear relationship ($p > 0.05$).
Significance level at $p < 0.05$, *; $p < 0.01$, **; $p < 0.001$, ***

4. Discussion

4.1 Temporal and spatial variations in soil physicochemical properties

There was an obvious spatial difference in most of the measured soil physicochemical properties, and flooding resulted in great temporal variation. Heterogeneity of soil physicochemical properties showed significant response to the elevation above the water level and the distance from the river channel. As the elevation increases away from the river channel, frequency, duration, and magnitude of flooding decrease, resulting in a significant spatial variation in soil moisture content (Geng et al. 2017). Such difference in moisture content also affects the conversion of aerobic-anaerobic condition and causes differences in nutrient availability (Hernandez and Mitsch 2007). Therefore, variations in moisture content among different elevations are accompanied by significant differences in several other soil physicochemical properties.

Conversion of aerobic-anaerobic condition induced by flooding alters biogeochemical reactions affecting nutrient availability (Goldberg and Gebauer 2009, Kim et al. 2012b). Biogeochemical reactions, especially for nitrogen, are sensitive to aerobic-anaerobic conditions of soil induced by flooding (Bowden 1987). Under anaerobic conditions, nitrification process which requires oxygen is limited, while denitrification (reduction of NO_3^- to NO, N_2O or N_2), dissimilatory nitrate reduction (conversion of NO_3^- to NH_4^+) or ammonification (conversion of organic N to NH_4^+) primarily occur. Therefore, the increase in NH_4-N concentration after flooding could be attributed to increasing dissimilatory nitrate reduction and ammonification, while

the decrease in NO_3-N concentration may be due to increasing denitrification and dissimilatory nitrate reduction under anaerobic condition. In addition, lower elevation in which soil is inundated permanently or periodically showed higher NH_4-N concentration in pre-flooding and post-flooding 1. This is also because of a decrease in oxygen leading to higher rates of nitrate reduction or ammonification. In post-flooding 2, both NO_3-N and NH_4-N concentrations increased, and it may be due to the decreased nitrogen uptake of plants since it was almost the end of the growth period. These findings confirm the importance of flooding on nutrient cycle in the riparian zone.

In the case of phosphorus availability, a decrease in PO_4-P concentration after flooding may be attributed to anaerobic conditions induced by flooding (Patrick and Khalid 1974). Phosphorus availability is closely related to the cycling of iron (Fe). Anaerobic conditions decrease the redox, thereby reducing Fe(Ⅲ) to Fe(Ⅱ), whose phosphate is more soluble. Increasing solubility leads to the release of associated phosphate. Once released, phosphate may move to water, therefore resulting in lower PO_4-P concentration after flooding (Badlwin and Mitchell 2000, de Vicente et al. 2010, Akpoveta et al. 2014). Furthermore, PO_4-P concentration showed significantly negative correlation with species richness (not shown as data) in pre-flooding, whereas no significant correlation was found after flooding. These results indicate that plant uptake under higher species richness plays an important role in PO_4-P concentration before flooding. This finding is consistent with the previous studies that vegetation affects PO_4-P concentration in wetlands (Silvan et al. 2004, Zhang et al. 2010). Flooding disturbance, however, alters the governing factor of PO_4-P concentration, leading to hydrological regime induced by flooding as a major determinant of PO_4-P concentration after flooding.

There were significant increases in pH and EC following the flooding. pH rise after flooding was commonly observed from previous studies that pH values of acid soils increase when flooded due to the consumption of protons for reduction of nitrate and Fe^{3+} (Ponnamperuma 1972, Quantin et al. 2001, Sun et al. 2007). Elevated EC due to flooding was also widely accepted in previous studies (Akpoveta et al. 2014, Wilson et al. 2015, Hafeez et al 2019). This may be attributed to inputs of soluble salts, ionic substance, and total dissolved solids carried by the flood.

Variations in elevation cause differences in sedimentation processes resulting in significant differences in organic matter content and soil particle distribution according to elevation. As high soil erosion occurs at higher elevation, and sedimentation are transported and deposited at lower elevation, organic matter content of high elevation was significantly lower than that of the other elevations. In other words, after flooding, organic matters transported from higher elevation can increase organic matter content at lower elevation (Peltoniemi et al. 2012). Furthermore, anaerobic condition of lower elevation, in which soil tend to be permanently or periodically flooded, may inhibit decomposition of soil organic matter, resulting in higher organic matter content.

In general, soil particle distribution is known as a static property, whereas in the riparian zone, soil particle distribution is affected by flow of water, flooding, erosion, and sedimentation processes (Middlekoop and Asselman 1998, Slattery and Burt 1997). Prior to flooding, soil particle distribution tends to be coarser at higher elevation. After flooding, overall soil particle distribution tends to be coarser, indicating that flood flow removed fine sediments from the riparian zone. Soil particle distribution can also affect nutrient availability. Phosphorus is adsorbed onto the solid surfaces (Toda et al. 2005), and fine particles provide large surface area per unit volume, resulting in large amount of adsorbed phosphorus. In pre-flooding, PO_4-P

concentration of low elevation, in which soil particle distribution is finer, was higher than that of higher elevation, but it was not statistically significant difference. Also, fine-textured soil leads to anaerobic condition (Bollmann and Conrad 2004), leading to higher nitrate reduction and ammonification rates. Therefore, in pre-flooding, NH_4-N concentration of low elevation was higher.

4.2 Temporal and spatial variations in vegetation

Vegetation structure was affected by flooding, resulting in temporal and spatial variations. In the riparian zone, topographic factors including elevation above the water level and distance from the river channel were major factors affecting hydrological characteristics. As the elevation increases away from the river channel, frequency, duration and magnitude of flooding decrease. Such hydrological regime is a major determinant of species composition and distribution patterns in the riparian zone (Casanova and Brock 2000). In other words, variations in elevation and distance create spatial differences in hydrological regime, and such hydrological gradients control the establishment and development of vegetation in the riparian zone (Ferreira and Stohlgren 1999, Casanova and Brock 2000).

Species composition and distribution pattern of vegetation were different along the gradient of the elevation from the water level and the distance from the river channel. The riparian vegetation exhibits a zonation pattern perpendicular to the river channel, resulting in spatial variation of vegetation along the elevation. Zonation of vegetation is determined by hydrological regime and species differences in tolerance to floods or droughts (Shafroth et al. 2002, Auble et al. 2005). Low elevation sites, which tend to be permanently or periodically flooded, were dominated by a single species tolerant to floods, such as *Z. latifolia* and *P. thunbergii*. The growth of *Z. latifolia* responded positively to high water level (Byun et al. 2017), and it could survive in deep water up to 60 cm above the soil surface and grow well in shallow water, up to 30 cm (Yamasaki and Tange 1981). *Polygonum thunbergii* could survive as creeping stems, which are parallel with the water flow and firmly fixed to the ground, making new shoots rapidly resulting in recovery of their biomass after flooding (Kim et al. 2012a). Also, simple flooding during early or late vegetative

growth did not affect the formation of amphicarpic seeds as well as vegetative parts (Choo et al. 2014). On the contrary, obligate upland plants intolerant to flooding, such as *A. princeps, G. max* subsp. *soja,* and *H. scandens*, were widely distributed at high elevation. Invasive species, including *H. scandens* and *S. angulatus*, were also observed at higher elevation. At lower elevation, constant flooding disturbance might have suppressed invasive species, while at middle species, in which species composition was complex and various, native species utilize limited resources more completely, thus preventing invasion (McNaughton 1983).

In addition, species composition and distribution patterns were homogeneous at low elevation, and dominant species did not change significantly over period. In contrast, dynamic variations of vegetation were observed both temporally and spatially at higher elevations. These findings are consistent with previous studies showing the homogeneity of vegetation at low elevation and the wide range of variations found at higher elevation (Nakamura et al. 1997, Capon 2005, Jager et al. 2012). This is because, only a few species tolerant to flooding are able to dominate low-lying area, which experience high stress, without competition from other species, resulting in the homogeneity of vegetation. High elevation with low flooding disturbance, however, may enable various species to establish, so that biotic factors, such as competition, may also regulate the species distribution.

In this study, Simpson index showed a skewed unimodal pattern along the gradient of elevation with largest index occurring at the middle elevation of 60-80 cm. This result supports the intermediate disturbance hypothesis that species diversity would be highest at a moderate intensity of disturbance (Huston 1979). Only a few species tolerant to flooding can survive at low elevation, and thus species composition might have been simple. At higher elevation, however, in spite of increasing inhabitation candidates, increasing competition stress might have

decreased species diversity. Species diversity might have been enhanced by newly created microhabitats due to flooding at middle elevation. Furthermore, as flooding removes the preexisting vegetation, addition of newly arrived species fostered species diversity. Some previous studies were consistent with this study. Pollock et al. (1998) discovered a unimodal pattern between flood frequency and species richness in riparian wetlands in southeast Alaska. Lou et al. (2016) also reported a unimodal pattern between water table depth and species richness in floodplain wetlands in China. However, some previous studies reported results conflicting with this study. Most researchers found a linear relationship between hydrological gradient and species diversity or richness. Ferreira and Stohlgren (1999) found that species diversity and richness in lake, river, and stream in Brazil were negatively correlated with water level or duration of floods. Lite et al. (2005) reported that during the summer dry season, richness of herbaceous species declined with increasing ground-water depth, whereas following the summer monsoon rains and floods, herbaceous species richness increased with increasing elevation above the channel. Chen et al. (2006) reported decreasing trends of species diversity and richness with increasing distance from the river channel. Garssen et al. (2015), which conducted a meta-analysis to assess the effects of flooding on riparian plant survival, biomass, species composition and richness, found nine publications reporting a decrease in species richness, seven reporting an increase, and two reporting no significant effect. On the other hand, some previous studies discovered a bimodal pattern between hydrological gradient and species diversity or richness (Zhu et al. 2013, Xu et al. 2015). In this study, middle elevation showed the highest Simpson index while aboveground biomass was the lowest, whereas the opposite pattern was observed for low and high elevations. This result is consistent with the previous studies that species richness decreased when aboveground biomass increased (Garssen et al.

2017). It may be attributed to the fact that a small number of competitive species have grown rapidly with higher aboveground biomass, resulting in lower species diversity by inhibiting the growth of other species (Reader et al. 1994). This result indicates that different changing patterns of species diversity exist in different ecosystems due to variations of hydrological regime, species composition, and regional characteristics.

4.3 Effects of soil physicochemical properties on vegetation

Topographic factors including the elevation above the water level and the distance from the river channel were major factors affecting variations in vegetation. Besides, heterogeneity of soil physicochemical properties also has an effect on the vegetation characteristics (Vivian-Smith 1997). In this study, based on RDA, moisture content, organic matter content, pH, EC, and nutrient availability were found to govern species composition and distribution patterns (Figure 8). Moisture content was the primary factor driving vegetation patterns in a riparian zone as shown in other studies (Xu et al. 2015). Variations in soil moisture content are due to elevation above the water level and distance from the river channel. Many previous studies have reported that hydrological gradient including soil moisture content and water depth along the elevation was the primary factor determining vegetation (van Coller et al. 2000, Hupp and Rinaldi 2007, Yabe and Onimaru 2009). Several other soil physicochemical properties other than soil moisture content, such as organic matter content (Eskelinen et al. 2009), pH (Asada 2002), EC (Ladenburger et al. 2006), and nutrient availability (Wassen et al. 2003) also affected species composition and distribution patterns of vegetation, which is consistent with previous studies. In other words, variations in vegetation are formed by the combined effects of hydrological gradient and variations in soil physicochemical properties.

4.4 Temporal and spatial variations in soil enzyme activities

There were significant temporal and spatial variations in all measured soil enzyme activities along the elevation above the water level. Activities of BG, NAG, ACP, and ALP showed decreasing trends with higher elevations. This finding is consistent with other studies showing that more flooded soil conditions stimulated soil enzyme activities. A'Bear et al. (2014) demonstrated that BG, NAG, and ACP activities were greater under wetting than drying. Geng et al. (2017) reported that BG, NAG, ACP, and ALP activities were significantly higher when received long inundation. In contrast, there were some previous studies reporting results in conflict with this study. Kang et al. (1998) reported higher activities of BG, NAG, and ALP in dry soil than permanently or partially waterlogged soil. Wang and Lu (2006) found that waterlogging inhibited BG, ACP, and ALP activities, and a decrease of BG was enhanced with increasing waterlogging time. Zhongmei et al. (2008) presented ACP activity was decreased with the increase of water level. Guenet et al. (2012) reported that BG, NAG, ACP, and ALP activities were highest with intermediate moisture level and followed by moist soil then dry soil, which is partially consistent with this study.

After flooding, BG and ACP activities of low elevation increased in post-flooding 1. These findings indicate that flooding enhances activities of soil enzymes related to the mineralization of carbohydrates, such as cellulose or chitin (Wilson et al. 2011). In post-flooding 2, however, all measured soil enzyme activities decreased. Decreasing soil enzyme activities in post-flooding 2 may be attributed to a decrease in temperature. Soil temperature in pre-flooding and post-flooding 1 ranged from 23.36 to 33.85°C and 22.75 to 30.41°C, respectively, whereas soil temperature ranged from 17.92 to 19.57°C in post-flooding 2 (not shown as data). Given that soil

enzyme activities are likely to increase with temperature up to some optimum temperature, low temperature in post-flooding 2 may have lowered soil enzyme activities.

4.5 Effects of soil physicochemical properties and vegetation on soil biological properties

In the riparian zone, flooding can alter soil physicochemical properties and vegetation, leading to variations of the primary factors governing soil biological properties. Based on RDA, the main factors found to govern soil biological properties were soil moisture content, organic matter content, nutrient availability, pH, and aboveground biomass (Figure 11). Especially, soil moisture content was a major factor influencing soil biological properties both in pre- and post- flooding. Many previous studies also found soil moisture content to be a primary factor regulating soil biological properties (Brockett et al. 2012, A'Bear et al. 2014, Geng et al. 2017, Ou et al. 2019). Soil moisture is one of the most important environmental factors influencing soil microbial community structure and activities (Brockett et al. 2012). Changes in soil moisture content affect soil microbes through microbial mobility, nutrient availability and diffusion, and oxygen diffusion. Higher moisture content increases soil microbial growth and activity, thus leading to higher soil enzyme activities. Furthermore, flooding can significantly change moisture content, altering vegetation and soil physicochemical properties including oxygen availability, which can affect soil biological properties. Therefore, flooding appeared to affect the temporal and spatial variations in soil biological properties in both direct and indirect ways.

Organic matter content was found to be an important factor regulating soil biological properties (Wilson et al. 2011). Organic matters provide a source of food for soil microbes, and act as substrates stimulating soil enzyme release. In addition, organic matters are major nutrient sources for plant growth. It can also contribute to soil quality, water retention, and air/water infiltration. Since these factors are related

to soil microbial growth, organic matter content is known to be positively correlated with soil enzyme activities and microbial biomass (Geng et al. 2017).

Based on RDA, nutrient availability, especially PO_4-P concentration was one of the primary factors determining soil biological properties (Figure 11). Soil microbes secrete more soil enzymes to meet the demand for nutrients (Xu et al. 2017). Given that global mean soil C:N:P acquisition ratio is approximately 1:1:1 (Sinsabaugh et al. 2008), deviations from this ratio reflect relative microbial demand for nutrients. In this study, the ratios of BG/(ACP+ALP) and NAG/(ACP+ALP) ratios were <1 for all elevations during the study period, indicating lower P availability (Sinsabaugh et al. 2009). These findings suggest higher enzyme production toward acquisition of P compared to C and N. In other words, soil P is the limiting factor, therefore, regulating soil biological properties.

There were several other factors affecting soil enzyme activities, such as soil EC and soil particle distribution. After flooding, soil EC remarkably increased, and increasing EC might have inhibited the growth and metabolism of microbes (Degens et al. 2001). In other words, increasing EC could decrease soil enzyme activities. Soil particle distribution is also known as an important factor determining soil enzyme activities. Variations of soil particle distribution show differences in water and nutrient holding capacity and soil aeration, further affecting microbial activities (Thomsen et al. 2003, Qin et al. 2010). In pre-flooding, BG, NAG, and ALP activities showed positive correlation with sand content and negative correlation with silt content. These findings are consistent with previous studies showing fine fractions have higher enzyme activities than coarser fractions (Lagomarsino et al. 2012, Geng et al. 2017).

Among vegetation traits, aboveground biomass was the main factor

responsible for different soil biological properties. Changes in vegetation, such as aboveground biomass, species composition, and distribution patterns, following flooding might have led to the alteration in the quantity and quality of litters. This finding is consistent with previous studies that aboveground part of plants can serve as an important factor regulating the microbial community structure and activity by regulating inputs of organic C and other nutrients in the form of litter or root exudates (Zak et al. 1994).

In this study, plant species diversity or richness did not exhibit significant effects on soil enzyme activities. Recently, there have been increasing studies on the relationship between soil microbial properties and plant species diversity or composition. Zhang et al. (2010) reported that BG activity, which was affected by plant species richness, strongly depended on the presence or absence of plants in constructed wetlands, while ACP depended on plant species richness. On the other hand, Porazinska et al. (2003) found that protozoa were not responsive to any of the plant community traits, but some bacterial and nematode groups were affected by plant characteristics specific to a particular plant species. The relationships between soil microbial properties and plant species are still controversial, and the mechanisms of plant species impact on soil microbial properties are unclear.

Most previous studies reporting positive or negative correlations between plant species diversity and soil microbial properties have not considered the effects of plant species diversity alone. Rather, they have taken into account combined effects of plant species diversity and several other factors such as aboveground plant biomass or the quantity and the quality of litter. Meier and Bowman (2008) reported that soil C and N cycling during decomposition were controlled by the composition and diversity of chemical compounds within plant litter mixtures, rather than by simple metrics of plant species diversity. Many studies explained the positive

relationship between plant species diversity and soil microbial properties as a result of a higher plant productivity due to higher plant diversity, leading to higher amounts of organic C or nutrients entering the soil (Stephan et al. 2000, Rodríguez-Loinaz et al. 2008). In this study, however, aboveground biomass and species diversity showed inverse relationship, and thus synthetic effects of aboveground biomass and species diversity could not exist. Further researches are needed to determine the linkages that might exist between vegetation traits and soil microbial properties. Ecological understandings of the linkages between aboveground and belowground would provide essential information for the sustainable soil ecosystems.

4.6 Synthesis

In the riparian zone, flooding created temporal and spatial variations in hydrological regime, and flooding affected dynamic and complex feedback among soil, vegetation, and soil microbes (Figure 12). As the elevation increase away from the river channel, frequency, duration, and magnitude of flooding decrease, resulting in a decreasing trend of soil moisture content. Variations of hydrological regime, and consequently the variations in soil moisture content appeared to be the most important factors that influence the system of the riparian zone. Such difference in moisture content also affects the aerobic-anaerobic condition, and conversion of aerobic-anaerobic condition altered biogeochemical reactions affecting nutrient availability or organic matter content. As high soil erosion occurs at higher elevation and sedimentation are deposited at lower elevation, there were significant differences in soil particle distribution and organic matter content according to elevation.

On the other hand, species diversity showed a skewed unimodal pattern along the gradient of elevation, while aboveground biomass showed an increasing trend with higher elevation or a U-shaped distribution along the elevations. The riparian vegetation exhibited a zonation pattern perpendicular to the river channel and was affected by flooding, resulting in temporal and spatial variations of vegetation. Variations in hydrological gradients, species differences in tolerance to floods or droughts, and biotic factors including competition determine the zonation of vegetation in the riparian zone. Besides, heterogeneity of soil physicochemical properties, such as pH, EC, soil moisture content, organic matter content, and nutrient availability also had an effect on the vegetation characteristics.

There were great temporal and spatial variations in the activities of BG,

NAG, ACP, and ALP. There was only a temporal variation in microbial biomass, and there were no significant temporal and spatial variations in CO_2 efflux. Flooding altered soil physicochemical properties and vegetation, leading to variations of the primary factors governing soil biological properties. Soil moisture content was a major factor influencing soil biological properties both in pre- and post- flooding. Higher moisture content increases soil microbial growth and activity, thus leading to higher soil enzyme activities. Flooding enhanced activities of soil enzymes related to the mineralization of carbohydrates. Organic matters provide a source of food for soil microbes, and act as substrates stimulating soil enzyme release, positively correlated with soil enzyme activities and microbial biomass. As soil microbes secrete more soil enzymes to meet the demand for nutrients, soil P was the limiting factor regulating soil biological properties. Besides, soil EC and soil particle distribution also affected soil enzyme activities. Among vegetation traits, aboveground biomass was the main factor responsible for different soil biological properties. Changes in vegetation, such as aboveground biomass, species composition, and distribution patterns, following flooding might have led to the alteration in the quantity and quality of litters, further regulating the microbial community structure and activity.

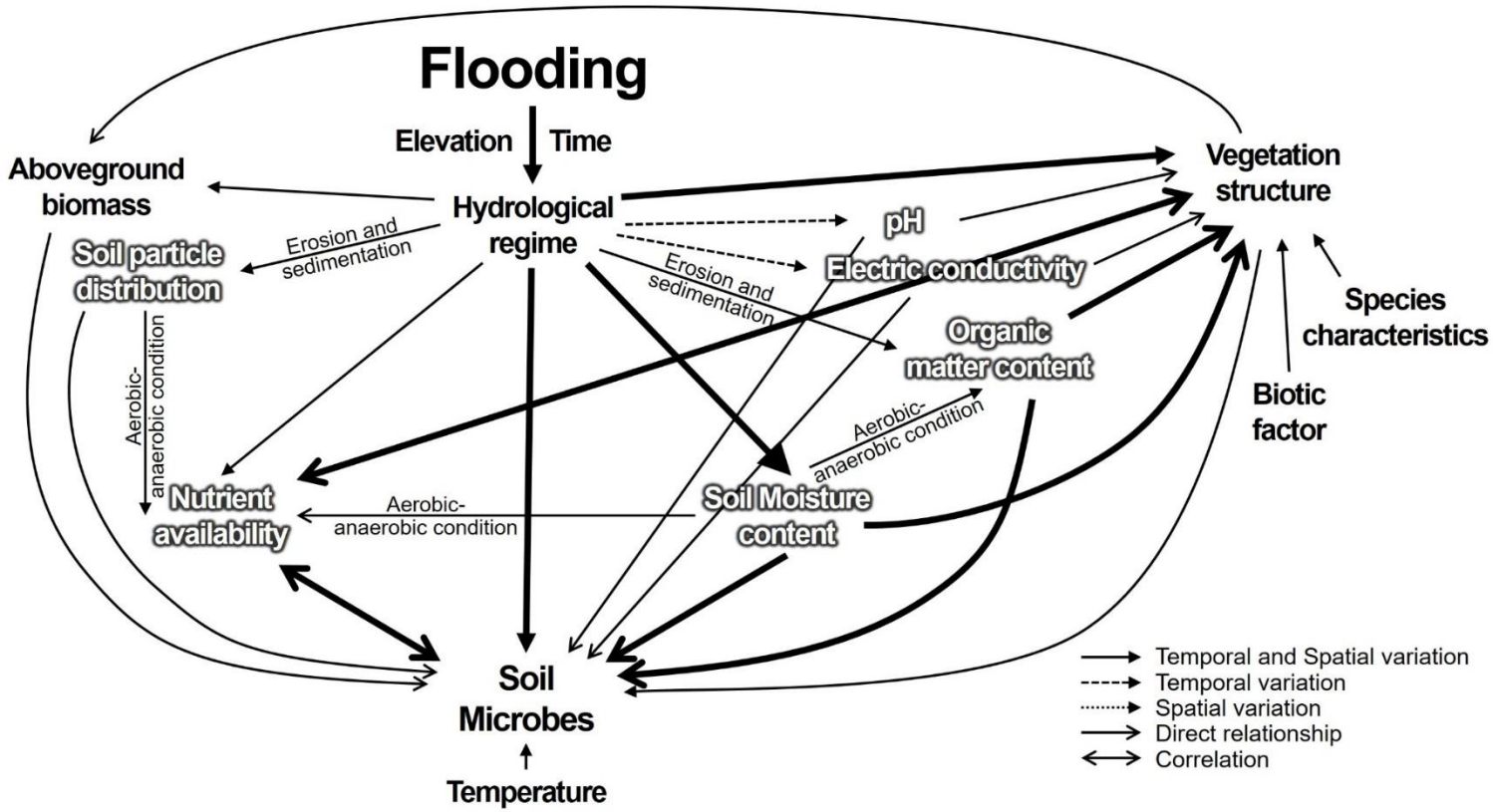

Figure 12. Schematic diagram of the relationships between flooding, soil physicochemical properties (pH, EC, soil moisture content, organic matter content, nutrient availability, and soil particle distribution), vegetation traits (vegetation structure and aboveground biomass), and soil microbes.

5. Conclusions

This study identified temporal and spatial variations of soil physicochemical properties, vegetation, and soil biological properties and the relationships among those three factors. In the riparian zone, flooding created hydrological gradient along the elevation above the water level, and variations of hydrological regime, and consequently the variations in soil moisture content appeared to be the most important factors that influence the system of the riparian zone. There were temporal and spatial variations in most of the measured soil physicochemical properties. The riparian vegetation exhibited a zonation pattern perpendicular to the river channel, and such variations in vegetation were formed by the combined effects of hydrological gradient, species characteristics, biotic factors and soil physicochemical properties. Flooding resulted in great temporal and spatial variations in most of the measured soil enzyme activities. Individual enzyme activity responded differently to flooding. Flooding altered the primary factors governing soil biological properties, and soil moisture content was a major factor influencing soil biological properties both in pre- and post- flooding. The other main factors governing soil biological properties were organic matter content, nutrient availability, especially P limitation and aboveground biomass. Further researches are needed to understand the linkages between aboveground and belowground for the sustainable soil ecosystems. These results indicate that effects of flooding on the overall system of the riparian zone is significant, and the effects depend on the variability of elevation. Based on these results, I conclude that variations of soil physicochemical properties, vegetation, and soil enzyme activities in the riparian zone are due to comprehensive changes in dynamic interactions between biotic and abiotic factors caused by flooding rather than solely due to the effects of flooding.

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국문 초록

하천변생태계는 토양 환경, 식생, 미생물 사이의 복잡한 되먹임 조절이 역동적으로 일어나는 곳으로, 범람에 따른 수문학적 특성의 변화는 이러한 되먹임 조절에 영향을 미쳐 하천변생태계의 생지화학적 순환에도 영향을 미칠 것으로 예상된다. 본 연구에서는 시간과 지형, 특히 수면으로부터의 고도와 수체로부터의 거리에 따라 하천변 토양의 이화학적 특성, 식생, 토양의 생물학적 특성이 어떻게 변화하는지를 파악하고, 토양의 이화학적 특성, 식생, 토양의 생물학적 특성의 관계를 종합적으로 파악하며, 토양의 생물학적 특성을 결정하는 주요한 요인을 파악하고자 하였다. 경기도 여주시 남한강 하천변생태계에 설치한 30개의 방형구를 고도에 따라 낮은 고도(Low), 중간 고도(Middle)와 높은 고도(High)로 나누어 토양의 이화학적 특성, 식생과 토양의 생물학적 특성(토양 효소 활성, 토양 미생물 생체량과 이산화탄소 플럭스)을 범람 전(pre-flooding: 6월)과 범람 후(post-flooding: 8월과 10월)에 조사하였다. 연구 결과, 범람은 고도에 따른 수문학적 기울기를 형성하였고, 토양 수분함량이 하천변생태계의 토양 및 식생 특성을 결정하는 가장 중요한 요인으로 작용하였다. 토양의 이화학적 특성과 식생은 시공간에 따른 유의한 변동을 보였다. β-glucosidase, β-N-acetylglucoasminidase, acid phosphatase과 alkaline phosphatase 활성은 고도가 증가함에 따라 감소하는 경향을 보인 반면, 토양 미생물 생체량과 이산화탄소 플럭스는 시공간에 따른 변동이 나타나지 않았다. 토양의 수분함량이 범람 전후에 토양의 생물학적 특성 차이를 결정하는 주요한 요인으로 작용하였으나, 시기에 따라 토양의 생물학적 특성에 영향을 미치는 요인에는 차이가 있었다. 유기물 함량, 가용성 양분과 식물의 지상부 생물량이

토양의 생물학적 특성 차이를 결정하였다. 이러한 결과는 하천변생태계의 토양의 이화학적 특성, 식생, 토양 효소 활성의 변화는 단순한 범람의 효과보다는 범람에 의한 생물적 요인과 비생물적 요인 사이의 되먹임 조절의 종합적인 변화에 의한 것임을 시사한다.

주요어: 고도, 범람, 생지화학적 순환, 수문학적 특성, 토양 미생물, 토양 수분함량

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