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Effects of Wetland Vegetation on Soil Microbial Composition: A Case Study in Tumen River Basin, Northeast China

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Abstract: Hydrology plays a dominant role in wetland plant distribution and microbial composition, but few studies explicitly attempted to relate the linkage between wetland vegetation and microbial community. The present study consisted of five wetland plant communities along three adjacent flood gradients zones (zone 1 dominated by *Carex appendiculat*, zone 2 dominated by *Eleocharis ovate*, and zone 3 dominated by *Phragmites australis/Bidens pilosa/Calamagrostis angustifolia*, which formed separate, monoculture patches). Gram negative and arbuscular mycorrhizal fungal phospholipid fatty acid (PLFA) are more abundant in the site with short flooding period (zone 3) than in the site with long flooding period (zone 1), and they are also different in the *P. australis*, *B. spilosa* and *C. angustifolia* of zone 3. Principle Component Analysis (PCA) showed that the flooding period could explain 92.4% of variance in microbial composition. Redundancy Analysis (RDA) showed that available nitrogen (AN), total nitrogen (TN) and soil organic matter (SOM) could explain the 79.5% of variance in microbial composition among *E. ovata*, *P. australis*, *B. pilosa* and *C. angustifolia*. Results demonstrated that flooding period was the main factor in driving the microbial composition and plant-derived resources could influence soil microbial composition in the seasonally flooded zones.

Keywords: plant soil feedback; redundancy analysis; phospholipid fatty acid (PLFA); soil property; flooding period

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1 Introduction

Wetlands provide many important functions and values, including wildlife habitat, biodiversity support, water quality improvement, flood abatement and carbon sequestration (Zedler and Kercher, 2005; Houlahan *et al*., 2006). Wetland plant communities play a fundamental role in maintaining these functions. Microbial communities maintain soil nutrient transformations, which in turn benefit the growth of wetland plant. But few study explicitly attempted to relate the linkage between wetland vegetation and microbial community. Because hydrology is considered as one of main factors shaping in the zonation patterns among plants (Van Eck *et al*., 2004), accumulation of plant biomass and growth of wetland plant at different water depths can vary significantly between species (Lanchlan *et al*., 2008). Hydrology also affects the wetland soil microbial composition (Gutknecht *et al*., 2006), because soil inundation could directly affect the soil redox status, availability of nu-

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trients, and many other biochemical and physical processes taking place in the rhizosphere (James *et al*., 2004). Further, the composition and function of the microbial communities have been shown to vary according to environmental conditions (Jaatinen *et al*., 2005). So it is very difficult to separate the effects of hydrology and wetland vegetation on the microbial community.

Plants can influence the abiotic and biotic conditions of soil, which in turn influence the performance of plants (Kulmatiski *et al*., 2008). These interactions have been widely considered as a driver of plant community dynamics (Kardol *et al*., 2013; Jing *et al*., 2015). Decaying vegetation provides the major source of carbon in wetlands; therefore any changes in plant biodiversity will directly influence the biochemical composition of soil organic matter and indirectly alter soil pH, nutrient availability and water retention (Reynolds *et al*., 2003; Kardol *et al*., 2006). Soil microbial communities play an important role in maintaining the functions of soils, such as decomposition, nutrient cycling, and nutrient acquisition (Wardle *et al*., 2004; Han *et al*., 2007). They are also sensitive to the changes in soil moisture, temperature and nutrient status (Zhao *et al*., 2011). Further studies showed that plants influence soil bacterial communities through the provision of carbon compounds (Schlatter *et al*., 2015), particularly through the availability of organically bound nitrogen. So the soil nutrient status could construct the linkage between plant community and soil microbial community in wetland.

Though researchers have studied the effects of hydrology on plants and microbial community in wetland, there is still a poor understanding of how wetland vegetation affects microbial composition due to the presence of water at or near the surface. In this study, in order to study the linkages between wetland vegetation and microbial communities and separate the effects of flooding disturbance and wetland vegetation on microbial community, we explored the soil microbial composition in five wetland plant communities along three zones. These zones were flooded during different periods of time and positioned adjacent to each other along a sloping gradient. And all samples were collected in the middle of September, when this study site was without flooding disturbance. Based on the study on wetland vegetation and microbial composition in different zones and same zone, we expected that different wetland plant communities would be associated with different soil microbial communities.

2 Materials and Methods

2.1 Study site and soil sampling

This study was carried out at a wetland of Jingxin Town (42°27′–42°40′N, 130°25′–130°39′E) in the Tumen River Basin, in the frontier region of China, D. P. R. Korea, and Russia. It is an important stopover site for migratory birds on the East Asia/Austaliasia Flyway. Wetland plant communities have a vital function in the living environment of migratory birds. It is necessary to study the linkage between wetland vegetation between microbial community, which ultimately determines ecosystem functioning and productivity.

Our experiment was conducted in three adjacent wetland vegetation zones dominated by five plant communities around a pond: 1) The *Carex appendiculata* zone was flooded more than five months every year. At the time of sampling, no aboveground biomass was present, but the remnants of the roots were still in the soil. 2) The *Eleocharis ovata* zone was flooded about three months every year. 3) The *Phragmites australis*/*Bidens pilosa*/*Calamagrostis angustifolia* zone was flooded one month every year. The three species formed separate, monoculture patches within the same zone.

All samples were collected in the middle of September 2014. Within each vegetation zone or patch dominated by each of the five species, three 1 m × 1 m quadrats were randomly placed at least 2 m away from each other. Plant species and coverage were described in each quadrat. Five soil cores were taken at 5–10 cm depth from each 1 m × 1 m quadrat, and combined to form one composite sample. Composite soil samples were divided into three subsamples, one sample for microbial analysis was placed in polyethylene bags and stored on ice; one sample for soil properties was sieved through a 2-mm mesh sieve and root fragments removed; and one sample for analysis of soil water content was sealed in polyethylene bags.

2.2 Soil properties analyses

Soil properties analyses followed Liu (1996). Soil-pH was determined on a 1∶2.5 (w/v) soil-water mixture. Soil water content (SWC, g of water per 100 g dry soil) was measured by oven-drying for 48 hours at 105℃. Soil organic matter (SOM, g/kg dry soil) was deter-

mined by the dichromate oxidation method. Total nitrogen (TN, g/kg dry soil) was calculated with an ultravio let spectrophotometer after Kjeldahl digestion. Available nitrogen (AN, mg/kg dry soil) was measured with alkali diffusion. Available phosphorus (AP, mg/kg dry soil) was determined by sodium hydrogen carbonate solution-Mo-Sb anti spectrophotometric method. Available potassium (AK, mg/kg dry soil) was measured with ammonium acetate extraction-flame photometric spectrophotometry.

2.3 Microbial analyses

Soil microbial communities were measured with phospholipid fatty acid (PLFA) analysis. PLFAs were extracted based on the procedure of Frostegard *et al*. (1991). Concentrations of each PLFA were calculated based on 19:0 internal standard concentrations. The PLFAs used as Gram-positive bacteria biomarkers were iso- and anteiso-branched saturated fatty acids (i14:0, i15:0, a15:0, i16:0, i17:0, a17:0); the PLFAs used as Gram-negative bacteria biomarkers were cyclopropyl (cy17:0, cy19:0), monounsaturated (16:1w7c) and straight chain fatty acids (14:0, 15:0, 17:0); the PLFAs bacterial biomarkers were i14:0, i15:0, a15:0, i16:0, i17:0, a17:0, cy17:0, cy19:0, 16:1w7c, 14:0, 15:0, 17:0, and the methyl branched 10Me16:0, 10Me17:0; the PLFAs used as fungal biomarkers were 18:2w6,9; the PLFAs used for actinomycetes were 10Me18:0 and for arbuscular mycorrhizal (AM) fungi were 16:1w5c (Djukic *et al*., 2010).

2.4 Statistical analyses

All data manipulation and statistical analyses were carried out using Microsoft Excel 2007 and SPSS 18.0. Differences between groups were tested by one-way analysis of variance (ANOVA) and comparisons among means were made using the least significant difference (LSD) test calculated at $P < 0.05$. Ordination analyses (Redundancy Analysis (RDA) and Principle Component Analysis (PCA)) were conducted using Canoco4.5 software.

3 Results

3.1 Characteristics of wetland plant community and soil

The characteristics of the wetland vegetation under different plant communities are shown in Table 1. In the *C. appendiculata* zone, aboveground biomass was not present, but the roots were still in the soil. In any of the vegetation zones/patches the companion plant species did not cover more than 9% of the surface area, while the dominant living plant species covered up to 100%.

Soil properties under different wetland plant communities are shown in Table 2. The soil-pH was slightly acidic ranging from 5.5 to 5.7. APs of five plant community

Table 1 Basic characteristics of wetland plant communities

Zone	Dominant plant species	Companion plant species	CD (month)	CDP (%)	CCP (%)	ABDP (g/m^2)
1	*C. appendiculata*	none	5	0	0	0
2	*E. ovata*	*Rorippa palustris*, *Ploygonum lapathifolium*	3	80	5	34.6 (7.2)
3	*P. australis*	*Carex rhynchophysa*, *Calamagrostis angustifolia*	1	95	9	133.5 (17.8)
3	*B. pilosa*	*Carex rhynchophysa*, *Bidens maximowicziana*	1	90	4	85.4 (11.5)
3	*C. angustifolia*	*Eragrostis cilianensis*, *Bidens pilosa*	1	100	6	97.5 (12.4)

Notes: CD, water disturbance; CDP, coverage of dominant plant species; CCP, coverage of companion plant species; ABDP, aboveground biomass of dominant plant species, values in blankets are standard deviation.

Table 2 Soil properties of five plant communities

Plant community	pH	Total nitrogen (g/kg)	Soil organic matter (g/kg)	Available nitrogen (mg/kg)	Available phosphorus (mg/kg)	Available potassium (mg/kg)	Soil water content (%)
C. appendiculata	5.5(0.1)ab	2.2(0.4)b	55.9(3.1)b	215.3(25.2)a	46.5(3.4)a	78.0(17.5)b	144.5(10.3)a
E. ovata	5.6(0.20)ab	1.4(0.1)c	26.4(0.3)c	113.7(6.0)b	43.7(0.2)a	105.3(19.9)a	76.0(6.0)c
P. australis	5.7(0.5)a	2.6(0.1)b	55.4(1.0)b	219.0(10.0)a	41.3(3.2)a	110.0(25.1)a	51.1(6.6)d
B. pilosa	5.2(0.1)b	2.4(0.2)b	54.0(2.1)b	160.7(30.5)b	44.7(7.0)a	64.3(14.6)b	85.2(2.2)b
C. angustifolia	5.6(0.2)ab	3.4(0.8)a	77.8(1.5)a	249.7(35.8)a	45.7(6.6)a	112.3(9.0)a	77.9(6.7)c

Notes: Values are arithmetic means ± standard deviation ($n = 3$). Different letters indicate significant differences ($P < 0.05$; ANOVA, Duncan's test).

soils were in same level at 44 mg/kg or so. TN ranged between 1.4 g/kg and 3.4 g/kg. SOM ranged between 26.4 g/kg and 77.8 g/kg. AN ranged between 113.7 mg/kg and 249.7 mg/kg. AK ranged between 64.3 mg/kg and 112.3 mg/kg.

3.2 Microbial community composition

The numbers of each microbial biomarker of five plant community soils are shown in Fig. 1. In total, the number of bacteria was the highest, followed by AM fungi and the other fungi, and lastly actinomycetes. There were also differences between plant community soils (Fig. 1 and Fig. 2). The bacterial PLFAs in soil of *P. australis* and *C. angustifolia* were almost the same, and were not significantly different from each other, as was the case for *E. ovata* and *B. pilosa* Gram positive and Gram negative PLFAs were lowest in *C. appendiculata* soil, and were different in *P. australis*, *B. pilosa*, *C. angustifolia* soils of zone 3. The ratio of Gram-negative to Gram-positive bacteria of soil in *E. ovata* was not significantly different from *C. appendiculata* soil and *P. australis*, *B. pilosa*, *C. angustifolia* soils (Fig. 2).The actinomycetes PLFAs of soil were highest in *P. australis* soil and least in *C. appendiculata*, the ratio of bacteria to actinomycetes was significantly different from the others ($P < 0.05$). The AM fungal and other fungal PLFAs of soil were highest in *C. angustifolia* and lowest in *C. appendiculata*, and the ratio of bacterial to fungal was not significantly different between the five plant community soils.

We used PCA to analyze 17 microbial phospholipid fatty acids in 15 soil samples of five wetland plant communities, which showed a clear separation along flood gradients (Fig. 3). Most variation was explained by PC1 (92.4%) and PC2 (3.6%), PC1 being the main factor in driving microbial community composition. Compared with zones with different flooding times, PC1 could be well explained by flooding period, and PC2 stands for other factors.

3.3 Relationship between soil properties and microbial composition

The *C. appendiculata* was already dead. In order to analyze the effects of wetland vegetation on soil properties

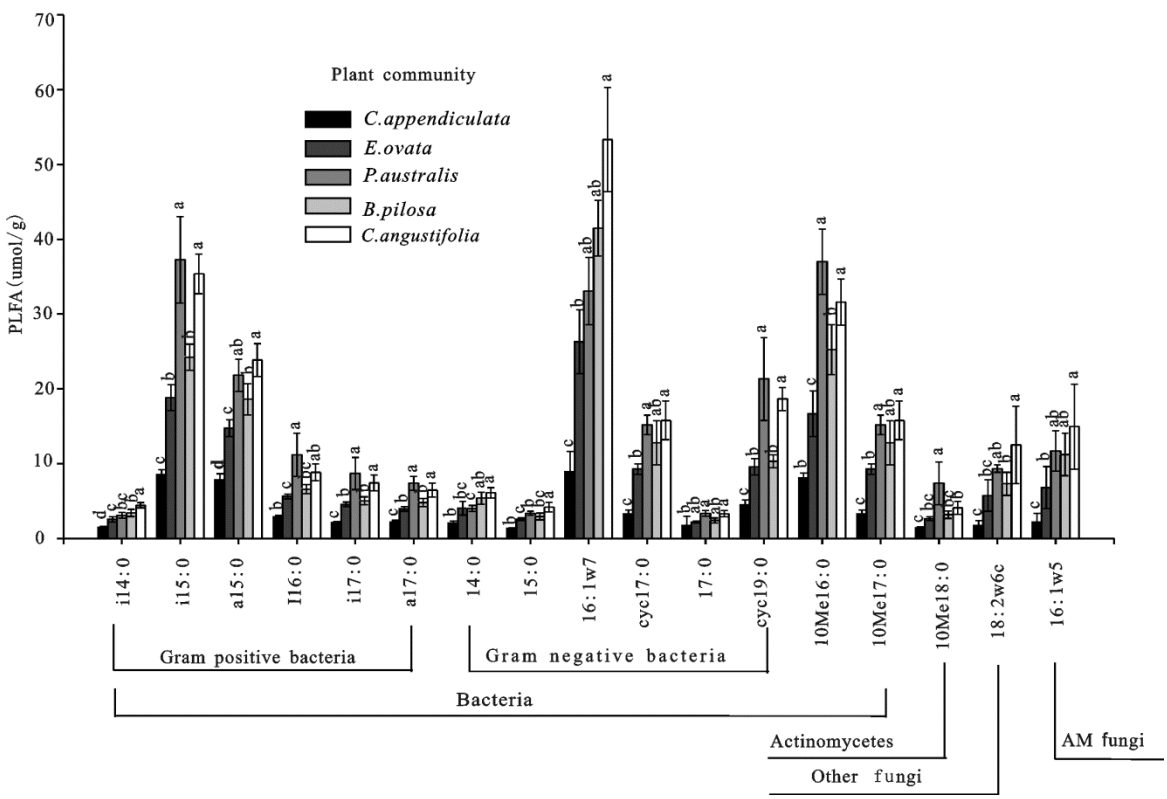

Fig. 1 Bacterial, actinomycetal and fungal phospholipid fatty acids (PLFAs) under five wetland plant communities. Values are arithmetic means ± standard deviation ($n = 3$). Different letters indicate significant differences ($P < 0.05$; ANOVA, Duncan's test). AM fungi, arbuscular mycorrhizal fungi

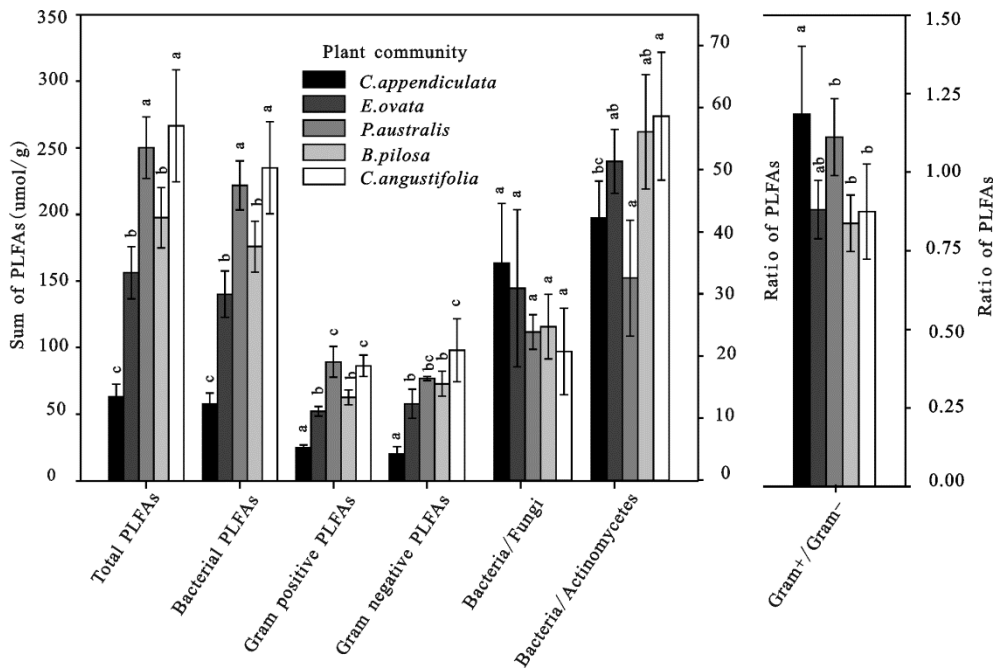

Fig. 2 Sums and ratios of phospholipid fatty acids (PLFAs) of various microbial groups in soils (0–10 cm depth) in studied site. Values are arithmetic means ± standard deviation (n = 3). Different letters indicate significant differences (P < 0.05; ANOVA, Duncan's test)

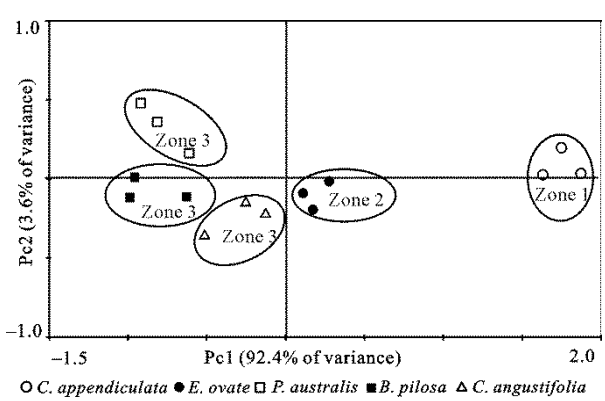

Fig. 3 Scores plot of principal component analysis showing separation of five studied sites with 17 microbial phospholipid fatty acids (umol/g)

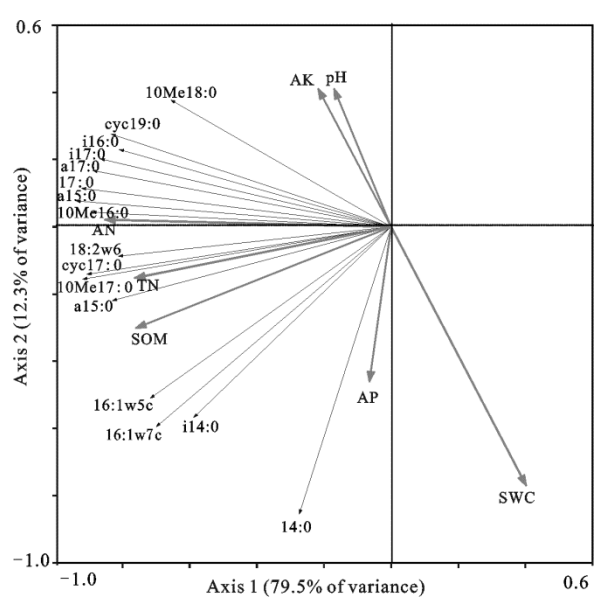

Fig. 4 Redundancy Analysis (RDA) of ordination diagram (Axis 1 × Axis 2) with microbial species and abiotic variables. AN, available nitrogen; TN, total nitrogen; SOM, soil organic matter; AP, Available phosphorus; AK, available potassium; SWC, soil water content

and microbial communities, we chose 12 data of soil properties and the composition of microbial communities from *E. ovata*, *P. australis*, *B. pilosa*, and *C. angustifolia*.

Seven indicators of soil used in the RDA explain 91.8% of the variance in microbial composition of the four wetland vegetation zones (Fig. 4). For the RDA ordination (Fig. 4), the first axis explained 79.5% of the species variation. Axis 1 was strongly correlated with AN, SOM and TN. The axis 2 explained 12.3% of species variation. Axis 2 was strongly correlated with SWC.

4 Discussion

Hydrology plays a dominant role in controlling microbial processes in wetlands. In general, higher water lev-

els increase the rates of anaerobic processes, for example, denitrification decreases the rates of aerobic processes (Balasooriya *et al*., 2008). Fluctuations of water levels create aerobic and anaerobic conditions in wetlands, controlling vegetation composition and microbial composition and activity in wetland soils. Balasooriya *et al*. (2008) using a $^{13}CO_2$ tracer, showed that Gram negative bacterial communities were relatively more abundant in the surface soils of the drier upper site than in the surface soils of the wetter lower site. In our study, Gram negative PLFAs were lowest in zone 1 (wetter site), and highest in zone 3 (drier site) (Fig. 2). We also used PCA to analyze the microbial composition in five plant communities, which showed that flood period was the main factor in driving the microbial composition and the soil microbial composition was also different among the *P. australis*, *B. pilosa* and *C. angustifolia* in zone 3 (Fig. 3). It showed that changes in microbial community structure followed not only the hydrological conditions but also the change of vegetation. This is consistent with Jaatinen *et al*. (2007), who reported that microbial communities changed significantly following water level drawdown and pattern of vegetation change in boreal peatland. Yang *et al*. (2010) studied the influence of water level gradient on marsh soil microbial activity of *C. angustifolia*, which demonstrated that microbial community changed and microbial activity decreased by increasing the level of waterlogging. Massaccesi *et al*. (2015) set up an experiment of grassland community that manipulated three attributes (the identity of dominant plant species, evenness, and spatial arrangement), and it appeared that dominant species identity was the main driver of soil microorganisms. Mycorrhizal fungi have also been found that they are very sensitive to high water levels (Rickerl *et al*., 1994), and also sensitive to plant community structure (Miller and Bever, 1999) that has been clearly demonstrated that plant species composition is important for arbuscular mycorrhizal fungal (AMF) colonization (Inhgam and Wilson, 1999). In our study, the AMF was the lowest in zone 1, and highest in zone 3, at the same time the AMFs were different in *P. australis*, *B. pilosa* and *C. angustifolia* soils in zone 3. In turn, it also showed that both flooding period and plant species are the main factors in driving AMF.

The relationship between microbial composition and vegetation was also been widely studied. Mitchell *et al*. (2012) assessed whether vegetation composition and soil chemistry explain the same or different parts of the variation in the soil microbial community. That study demonstrated that plant community composition and soil chemistry each uniquely explains the inertia in the archaeal terminal restriction fragment length polymorphisms (TRFLPs), bacterial TRFLPs, fungal TRFLPs and all PLFAs. So plant species effects based on their nutrient content might prove helpful as a framework for this understanding. In our study, we used RDA to analyze the relationship between soil properties and microbial communities in *E. ovata*, *P. australis*, *B. pilosa*, and *C. angustifolia* soils. This showed that AN, SOM and TN were the main drivers in microbial community composition (Fig. 4). SOM in natural wetlands is mainly from the decomposition of animal and plant residues (Reddy and Patrick, 1975). Bardgett and Shine. (1999) pointed out that plant communities could modify the development of soil properties by providing resources in litter. Bai *et al.* (2005) reported that wetland plant litter inputs affect the spatial distribution of SOM. SOM was also found to significantly correlate with soil texture (Bruland and Richardson, 2004). Plant N uptake can influence bacterial community structure by mediating the timing and magnitude of soil N availability (Colin *et al.*, 2015). Plant species can have large impacts on ecosystem nitrogen cycling, and species impacts are not caused by differences in plant quantity and quality, but by plant species impacts on nitrogen inputs and losses (Knops *et al.*, 2002). Bai (2003) studied the nitrogen transformation of wetland plants, which showed that available nitrogen affected the plant growth and the inputs and decomposition of litter contributed to nitrogen accumulation in surface soils. The SOM was related to TN. AN, SOM and TN could be considered as indicators of wetland plant between microbial communities. In our study, AN, TN and SOM in *E. ovata* soil were lower than those in other plant community soils, so as the aboveground biomass. Wardle *et al*. (2004) pointed out that plants provide both the organic carbon for decomposer subsystems and the resources for root-associated organisms such as roots herbivores, pathogens, and symbiotic mutualists. Plant species also play an important role in structuring soil bacterial communities in forest (Bach *et al.*, 2010). Weand *et al.* (2010) further reported that both the composition of microbial community and enzyme activities vary with different vegetation types in forest. Our results are in agreement with those

findings.

Although duration of flooding could affect the distribution of plant (Lou *et al*., 2013), wetland plants have evolved adaptation mechanisms that enable them to survive in the low oxygen supply and aeration of roots would enable them to survive periodic soil saturation and the accompanying changes in soil chemistry (Jackson and Armstrong, 1999). Bacterial composition and diversity corresponded strongly with soil pH, land use and restoration status (Wyatt *et al*., 2008). Moche *et al*. (2015) studied monthly dynamics of microbial community structure and their controlling factors in floodplain soils, and showed that stable properties of bulk soil such as oil organic carbon, soil texture, and associated flood fluctuation had a stronger impact on soil microbial composition than monthly fluctuations. Wang *et al*. (2015) pointed out that geographic distance and climatic factors concurrently govern bacterial biogeographic patterns. Their study sites were on a larger scale and in different kinds of wetland types, and different levels of restoration. In our study we focused on the relationship between plant community and microbial composition and isolated the influence of the water fluctuation. Our study site was on a small-scale and focused on the variance of wetland plant communities, and demonstrated the linkage between wetland vegetation and soil microbial composition.

5 Conclusions

The objective of this study was to study the linkages between wetland vegetation and microbial communities and separate the effects of flooding disturbance and wetland vegetation on microbial community. The study was carried out in five plant communities of three adjacent flooding periods in September, when this study site was without flooding disturbance. Microbial community structures were investigated by PLFA technique. The AM fungal and Gram negative PLFAs were higher in drier site, and different in the *P. australis*, *B. pilosa* and *C. angustifolia* soils in zone 3, showing that flooding period and plant species both affect the microbial composition. Based on PCA, flooding period could explain the 92.4% of variance in microbial composition, so the flooding period is the main factor in driving the microbial composition. Based on RDA between soil properties in different plant community soils and associated microbial composition, it was showed that AN, SOM and TN could explain the 79.5% of variance in microbial composition, and the plant-derived resources were significantly relative with AN, SOM and TN.

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