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RESEARCH ARTICLE

Factors controlling organic carbon distributions in a riverine wetland

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Abstract

As a significant reservoir of organic carbon (OC), natural wetlands play an important role in mitigating greenhouse effects. To determine what factors might influence OC, we analyzed the distributions of dissolved organic carbon (DOC), light fraction organic carbon (LFOC), and heavy fraction organic carbon (HFOC) in sediments taken from the Yanghe River Wetland (YRW) and assessed the effects of several environmental variables on the distribution of the different carbon types. The microbial community abundances and compositions of the sampled sediments were analyzed by 16S rRNA amplicon sequencing. Redundancy analysis (RDA) was used to reveal the environmental factors that affect the distribution of OC. The DOC and LFOC contents varied significantly in the research area, while HFOC content showed no variation. The DOC content was significantly affected by sediment pH, vegetation height, and microbial abundances, and the LFOC content was significantly affected by water pH. We also proposed a novel indicator to study the microbial effect on the distribution of OC content in wetlands: weighted abundance of related microbes (WARM). This study identifies the environmental factors that could affect the distribution of OC in a riverine wetland and outlines the calculation of a novel indicator.

Keywords Controlling factors · Dissolved organic carbon · Light fraction organic carbon · Heavy fraction organic carbon · Riverine wetland · Weighted abundance of related microbes

Introduction

Global warming is the consequence of excessive anthropogenic greenhouse gas emissions (e.g., CO_2 and CH_4) and has caused serious environmental problems globally (Florides and Christodoulides 2009; Vitousek 1994). Wetland ecosystems play an important role in mitigating the greenhouse effect by offsetting the release of CO_2 (Lehmann 2007). As organic carbon (OC) reservoirs (Cao et al. 2015a; Gałka et al. 2018), wetlands hold up to 20–25% of the total carbon stock in terrestrial soils globally (Zhang et al. 2008). Riverine wetlands sequester photosynthesized carbon in their sediments, which has significant effects on the distribution of OC (Hope et al. 1994; Liu et al. 2017). Hence, identifying the distribution of OC in wetlands and the affecting factors controlling this distribution may provide novel insights for the evaluation of ecosystems and carbon cycling.

According to its solubility, OC can be divided into two primary components—dissolved organic carbon (DOC) and particulate organic carbon (POC); POC can be further divided into light fraction organic carbon (LFOC) and heavy fraction organic carbon (HFOC) based on its density. In general, DOC is produced by the decomposition of plant and animal residues (Haynes 2000) and is composed of organic acids, particularly humic acid (Vance and David 1992). The LFOC (density ≤ 1.7 g/cm^3) is mainly composed of incompletely decomposed residues (Janzen et al. 1992) and can be easily decomposed by microbes into CO_2 or CH_4, and its distribution is affected by several environmental factors (Hedges et al. 2000; Janzen et al. 1992; Xu et al. 2014). The HFOC (density ≥ 1.7 g/cm^3) is stable and not easily mineralized (Tan et al. 2007). It acts as the primary form of OC stored in sediments (Barrios et al. 1996), and its particles are always larger than those of LFOC and DOC (Ebrahimi et al. 2017). Different types of OC

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components have different properties, and DOC, LFOC, and HFOC have been extensively studied to better understand their distributions and influencing factors.

The distribution of OC in riverine wetland systems might be affected by multiple environmental factors (Cao et al. 2015b). For example, vegetation litterfall, the main source of OC and contributor to soil texture, can affect the content of OC by influencing the movement of water in soil (Da Costa et al. 2016), and temperature can affect leaching of OC from rocks and soils (Selemani et al. 2018). An important influencing factors on the content of OC in wetland sediments is pH due to its influences on the activity of OC-related microbes and the coagulation and ionic exchange of OC-related cations (Li et al. 2019; Strehse et al. 2018; Sugihara et al. 2015). Although the influence of pH on OC has been revealed, its influence on the different types of OC remains unclear. Moreover, the relative effects of water and sediment pH on the three types of OC have not been investigated. Wetland vegetation and microorganisms, which are considered important factors determining the distribution of OC, serve as the producers and the consumers of OC (Cao et al. 2017b; Villa et al. 2014; Wang et al. 2011). Although microbes influence the distribution of OC, there is a lack of research on how to objectively reflect the effects of different microbial taxa on distribution patterns of OC in riverine wetlands.

The Yanghe River Wetland (YRW) is a typical riverine wetland with a long history, making it an ideal study site to investigate the influence of environmental factors on accumulated OC over time. In this study, the distribution of LFOC, HFOC, and DOC, and related environmental factors, including the composition and structure of microbial communities, in the YRW were assessed.

The main goals of the study were (1) to study the distribution of OC, (2) to reveal major factors influencing the distribution of OC in riverine wetlands, and (3) to present a new indicator that can be used to describe the microbial effects on the distribution of OC.

Materials and methods

Site selection and field sampling

The Yanghe River, located in Xuanhua District, Zhang Jiakou City, Hebei Province, China, is the main tributary of the primary standby potable water source for Beijing—Guanting Reservoir. The river has a catchment area of 9762 km^2, and the soil types are fluvo-aquic, calcareous-cinnamon, fluvo-cinnamon, and meadow-windy sandy. The soil of the Yanghe River has great absorption capacity (Xu et al. 2011), making it an ideal carbon pool. As a river that has undergone several well-known pollution events (Li 2014), assessing its organic carbon distribution could provide better information on riverine ecosystems and carbon cycling in rivers. However, to date, there has been little research into the OC of the Yanghe River. Our research area is the upstream of Yanghe River, where the soil type is sand. The research area was divided into three sections due to its length and diverse range of biotopes—the upper (40° 35′ 14″–40° 35′ 36″ N, 115° 1′ 19″–115° 2′ 12″ E), middle (40° 34′ 36″–40° 35′ 7″ N, 115° 2′ 45″–115° 3′ 48″ E), and lower sections (40° 33′ 12″–40° 34′ 33″ N, 115° 3′ 53″–115° 5′ 42″ E) (Fig. 1). The following biotopes were used to determine the influence of vegetation on the distribution of OC: *Echinochloa* biotopes (mainly consisting of *Echinochloa colonum* (L.) Li Link and *Echinochloa crusgalli* (L.) Beauv var. *crusgalli*), *Typha* biotopes (mainly consisting of *Typha latifolia* Linn, *Typha angustifolia* Linn, and *Typha minima* Funk), and bare land.

Field sampling was conducted in July 2018. Sediments and subsamples (sediment samples used for microbial analysis) were collected from *Echinochloa* biotopes and *Typha* biotopes, and bare land in the upper and lower sections. Due to dredging in the middle section of the river, sediments were only collected from two biotopes—the *Echinochloa* biotopes and bare land. *Typha* and *Echinochloa* samples were transported to the laboratory to measure the dry weight. We set four sampling points in every biotope, and at each sampling point, five-spot sampling in 1 × 1-m sampling sites was performed to collect sediments using a bottom sampler or soil auger. The five samples for each site were mixed to create a representative sample, and the collected sediments were put into sealed plastic bags individually and transported to the laboratory, where they were stored at 4 °C. The soil chemical properties were measured as soon as possible, within 2 days of collection. Simultaneously, subsamples were stored at − 20 °C for microbial analyses. Constant-weight aluminum specimen boxes were used to sample fixed-volume sediments. Water pH, dissolved oxygen (DO), water temperature, vegetation coverage, and vegetation height were also measured using a portable pH meter, a portable DO analyzer, and a ruler, respectively. A total of 32 bags of sediment samples, 32 bags of subsamples, 32 aluminum specimen boxes, and 24 bags of plant samples were collected from the research area.

Laboratory analyses

Physicochemical analyses

To measure the bulk density of the sediments, the aluminum specimen boxes were dried in an oven at 105 °C until their weight was constant. To measure the sediment pH, a pH meter (PHS-2F, REX, China) was used at a 1:5 ratio of fresh sediment to 0.1-mol/L KCl solution. Before further analyses, sediment samples were ground and dried at room temperature and then sieved using a 0.9-mm sieve to assess OC content. To assess the DOC content, we followed the methods of Dittmar

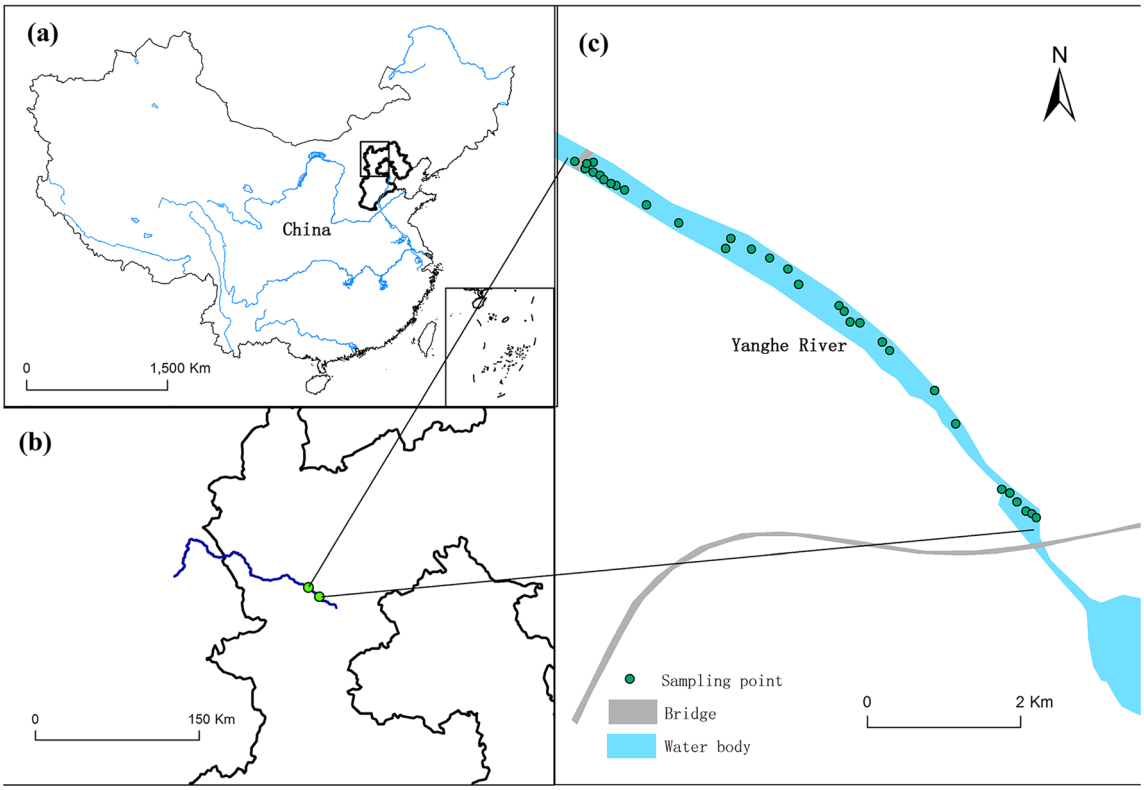

Fig. 1 Research area and sample spots. a Map of China. b Picture of the whole Yanghe River. c The research area and the distribution of sample spots

et al. (2008) and Jones and Willett (2006). Sieved and half-dried sediment samples (10.00 g) were weighed and placed in 100-mL constant-weight polyvinyl-labeled bottles. Filtrated supernatant, which was extracted from the sediment using a potassium chloride solution (0.1 mol/L), was analyzed using a total organic carbon (TOC) analyzer (TOC-L, Shimadzu, Japan). To measure the LFOC and HFOC content, the methods of Zhang et al. (2005b) were followed. Samples were separated into LFOC and HFOC using a sodium iodide solution (1.70 g/mL). The LFOC was washed with diluted hydrochloric acid (1:10) several times after being filtrated into 0.043 brass sieves. Then LFOC was flushed with a calcium chloride solution (0.1 mol/L) and distilled water. The HFOC was washed with diluted hydrochloric acid (1:10), calcium chloride solution (0.1 mol/L), and distilled water at least 6 times. After the elution of inorganic carbon and elimination of chloride ions, dry sediments were analyzed using an element analyzer (Vario EL III, Elementar Analysensysteme, Germany). *Typha* and *Echinochloa* samples were dried to a constant weight at 75 °C in an oven prior to weighing.

DNA extraction, amplification, and sequencing

DNA was extracted from every sediment sample using the cetyl trimethyl ammonium bromide (CTAB) method. Briefly, the samples were added to 20-μL lysozyme and 1000-μL CTAB buffer in 2.0-mL EP cells. After water-bath heating at 65 °C for 3 h, 950-μL supernatant of every centrifuged sample was mixed with phenol (pH 8.00):chloroform:isoamyl alcohol (25:24:1). The mixed sample was centrifuged (12,000 rpm, 10 min), and the DNA was extracted with chloroform:isoamyl alcohol (24:1) and precipitated with isopropanol at − 20 °C. Then, 75% ethanol was used to wash the precipitates twice before they were dissolved in 51-μL ddH2O. Finally, to digest RNA, 1-μL RNase A was added at 37 °C for 15 min (Zhang and Wang 2017). Electrophoresis on 1% agarose gel was used to examine the DNA purity, and the DNA concentration was determined using a NanoDrop ND-1000 UV-Vis spectrophotometer (Thermo Fisher Scientific, Waltham, MA, USA). The qualified samples were used as the template after they were diluted to 1 ng/μL. Polymerase chain reaction (PCR) amplification of the V4 hypervariable regions of the microbial 16S rRNA gene was performed. The barcode and primer sequences we used were 515F (GTGYCAGCMGCCGCGGTAA) and 806R (GGACTACNNGGGTATCTAAT). During the process, the efficiency and accuracy of amplifications were ensured by using Phusion High-Fidelity PCR Master Mix with GC Buffer (New England Biolabs, Ipswich, MA, USA) and efficient high-fidelity enzyme. The 1% agarose gel electrophoresis was conducted once more to detect the PCR products. Then, the sample was pooled and purified with a Qiagen Gel Extraction Kit (Qiagen GmbH, Hilden, Germany). To generate sequencing libraries, the TruSeq DNA PCR-Free Sample Preparation Kit (Illumina, San Diego, CA, USA) was employed

and a Qubit 2.0 Fluorometer (Thermo Fisher Scientific) was used for quantification. After the size distribution of the libraries was analyzed with an Agilent2100 Bioanalyzer (Agilent Technologies, Palo Alto, CA), the library was sequenced on the HiSeq2500 (Illumina, San Diego, CA, USA) platform. Then, 250-bp paired-end reads were generated and assigned to samples based on their unique barcode. Reads were truncated by cutting off the barcode and primer sequence before they were merged using FLASH (V1.2.7, http://ccb.jhu.edu/software/FLASH/). To obtain high-quality, clean tags, the produced raw tags were filtered following the QIIME (V1.7.0, http://qiime.org/index.html) quality control process. After the filtration, tags were compared with a reference database (Gold database, http://drive5.com/uchime/uchime_download.html), and the UCHIME algorithm (UCHIME Algorithm, http://www.drive5.com/usearch/manual/uchime_algo.html) was employed to detect the chimera sequences. The effective tags were obtained after the removement of chimera sequences. To obtain operational taxonomic units (OTUs) for the calculation of relative abundance, a sequence analysis was performed using the UPARSE software (UPARSE v7.0.1001, http://drive5.com/uparse/). Sequences with ≥97% similarity were considered as the same OTU. The representative sequence of each OTU was screened, and the Silva Database (version 132; http://www.arbsilva.de/), using the RDP classifier (version 2.2, http://sourceforge.net/projects/rdp-classifier/), was used to annotate taxonomic information. The MUSCLE software (version 3.8.31, http://www.drive5.com/muscle/) was then used to investigate the phylogenetic relationship of different OTUs. Before further analysis, OTU abundances were normalized according to a standard of the sequence number corresponding to the sample with the least sequences. The relative abundance of microbes was calculated using the tag number of each OTU divided by the total number of tags of the OTUs (Figs. 2 and 3) (Caporaso et al. 2011; Fang et al. 2020; Hess et al. 2011).

Calculation of the weighted abundance of related microbes

Relative abundance has often been used to describe microbial community compositions. To objectively quantify the influence of OC-correlated microbial taxa on OC content, the identification of an indicator is needed to accurately reflect the effects of microbial abundance and community compositions on the distribution of OC. Therefore, the weighted abundance of related microbes (WARM) was created to represent the total influence of OC-correlated microbial abundance and community composition on the OC content. The following equation was used to calculate the WARM:

$$\mathrm{WARM} = \sum ri \times pi$$

where "*ri*" is the correlation coefficient between microbial abundance and OC content, and "*pi*" is the proportion of each microbial species in the communities of each site ($pi = Ai/At$, where "*Ai*" is the relative abundance of the focal taxon and "*At*" is the relative abundance of all microbial taxa whose abundances are correlated with OC). When $Ai \neq At$, we used the relative abundance of each microbe to determine the total

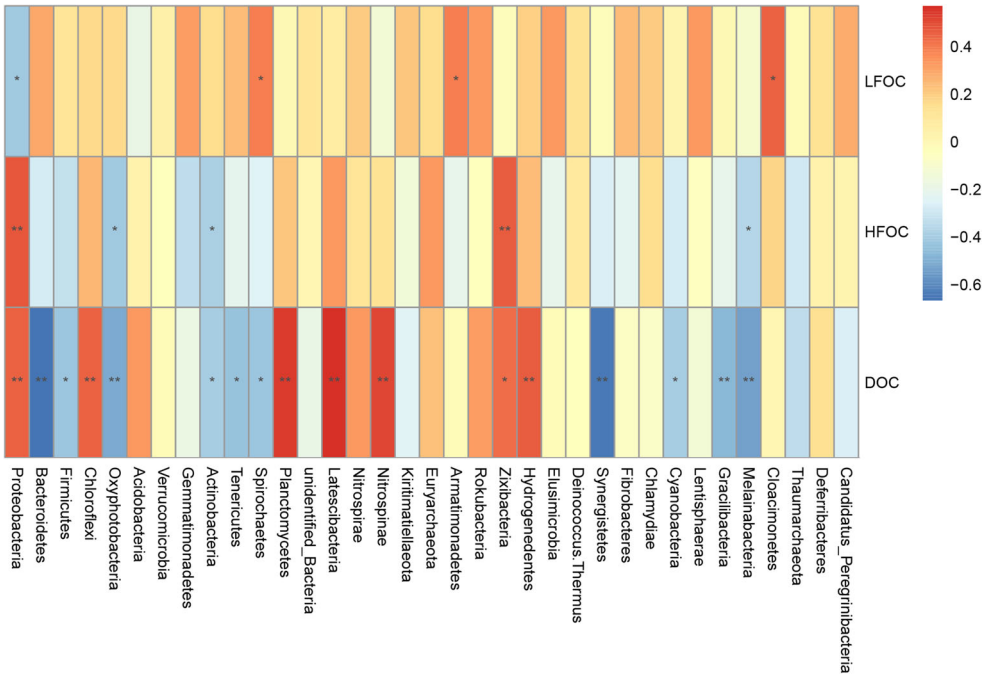

Fig. 2 Spearman correlations between microbes and organic carbon (OC) at the phylum level. Significantly correlations among microbial phylum and OC are represented by asterisks (**$p < 0.01$ and *$p < 0.05$). The red and blue ground colors reflect positive and negative correlations, respectively, among OC and microbial phylum, while the gradation of the color reflects the degree of correlation

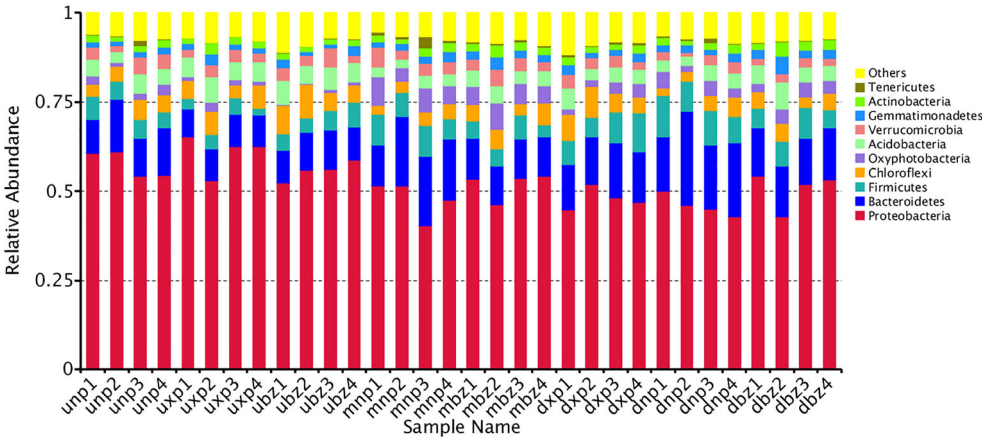

Fig. 3 Top 10 microbes at the phylum level and their relative abundances. "u" stands for upper section, "m" stands for middle section, and "d" stands for down section; "np" stands for bare land, "xp" stands for *Typha* biotopes, and "bz" stands for *Echinochloa* biotopes

relative abundance at each site. When $Ai = At$, we considered $pi = Ai$. Significant differences in the WARM were found ($p < 0.001$) among diverse sites. Correlation analysis between WARM and OC content suggested that WARM was significantly related to the OC content (Table 1).

Statistical analyses

One-way analysis of variance (ANOVA) was used to test for the significant differences in the distribution of DOC, LFOC, and HFOC in the *Echinochloa* biotopes, *Typha* biotopes, and bare land, and in the upper, middle, and lower sections. In addition, two-way ANOVA was used to test for the interaction effect between biotopes and locations on the distribution of OC. The Pearson correlation analysis was used to assess the correlations between the OC content and environmental factors. A redundancy analysis (RDA) based on the mean of 999 Monte Carlo permutations (1000 unrestricted random permutations; $p < 0.05$) was used to identify the most important factors controlling OC content among the factors that had a significant relationship with the OC content. The data were normalized during the RDA. One-way ANOVA, two-way ANOVA, Pearson's correlation analysis, RDA, and the construction of graphs were performed using SPSS v22.0, Canoco for windows v4.5, Origin v2017, and Canodra for windows v4.5.

Table 1 Two-tailed Pearson analysis of WARM and OC

	DOC	LFOC	HFOC
WARM(DOC)	0.573**		
WARM(LFOC)		0.375*	
WARM(HFOC)			0.497**

DOC, dissolved organic carbon; *LFOC*, light fraction organic carbon; *HFOC*, high fraction organic carbon

*Significant correlation when $p < 0.05$

**Significant correlation when $p < 0.01$

Results

Environmental factors and spatial distribution patterns of OC

The environmental factor data gathered during sampling and the laboratory analysis is shown in Table 2. Significant differences in the distribution of DOC were found in the three parts of the river ($p = 0.021$, Table 3; Fig. 4d). The DOC content in the middle section (25.43 mg/L) was significantly lower than that in the upper section (37.94 mg/L) but significantly higher than that in the lower section (23.47 mg/L). The DOC content varied significantly among *Echinochloa* biotopes, *Typha* biotopes, and bare land ($p < 0.001$, Table 3; Fig. 4a). *Typha* biotopes had the highest DOC content (44.27 mg/L) and bare land had the lowest (15.64 mg/L). The DOC content in the *Echinochloa* biotopes was 33.21 mg/L. The significant interactions suggest that the distribution of DOC was affected by more than one factor ($p = 0.013$, Table 3). The Pearson correlation analysis revealed that bulk density, sediment pH, dry weight of vegetation, DO, vegetation cover, and vegetation height were all significantly correlated with the DOC content (Table 4). The RDA revealed that the DOC content was significantly negatively associated with sediment pH, which accounted for 56% of the observed variation ($p = 0.002$, Fig. 5a). Vegetation height explained 21% of the variation ($p = 0.002$). The correlation analysis showed that DOC and WARM were significantly correlated ($p = 0.001$, Table 1). An RDA run with WARM, sediment pH, height of plants, and DOC content data showed that WARM was not an important factor in the interpretation of DOC ($p > 0.05$, Fig. 5b).

The LFOC content varied significantly among the upper, middle, and lower sections ($p = 0.027$, Table 3; Fig. 4f). The LFOC content in the middle section (35.6%) was higher than that in the lower section (29.5%), with the upper section having the lowest content (20.3%). However, there were no significant differences in the LFOC content among the *Echinochloa* biotopes, *Typha* biotopes, and bare land ($p =$

Table 2 Physical parameters of water and sediment in different sampling spots

	wpH	SD	wt	SD	DO	SD	bd	SD	spH	SD
unp	7.97	0.085	26.2	2.141	5.3	1.087	0.328	0.059	8.34	0.193
uxp	8.08	0.106	28.7	0.868	5.0	0.567	0.533	0.172	8.09	0.347
ubz	8.04	0.043	27.9	2.414	3.9	0.567	0.513	0.115	7.96	0.132
mnp	8.20	0.104	27.3	1.173	7.7	0.743	0.398	0.119	8.30	0.167
mbz	8.37	0.142	29.3	0.275	8.7	1.863	0.440	0.074	8.03	0.267
dnp	8.20	0.144	30.2	3.050	6.6	0.916	0.443	0.185	8.25	0.214
dxp	8.14	0.025	29.5	2.354	6.0	0.844	0.518	0.237	8.23	0.057
dbz	8.12	0.073	29.5	1.804	6.1	1.010	0.378	0.152	8.39	0.272

u, the upper part; *m*, the middle part; *d*, the down part; *np*, bare land; *xp*, *Typha* biotopes; *bz*, *Echinochloa* biotopes; *SD*, standard deviation; *wpH*, water pH; *wt*, water temperature; *DO*, dissolved oxygen; *bd*, bulk density; *spH*, sediment pH; and the unit of wt is degree centigrade

0.767, Table 3; Fig. 4b), and there were no significant interactions between variables in terms of the distribution of LFOC. The Pearson correlation analysis showed that the DO and water pH were significantly correlated with the LFOC content (Table 4). An RDA run using DO and water pH showed that the latter variable was the most important factor affecting LFOC distribution ($p = 0.012$, Fig. 5a), explaining 68% of the observed variation. The correlation analysis showed that WARM and LFOC were also significantly correlated ($p < 0.05$, Fig. 5b, Table 1).

Although the HFOC content in the upper section was higher than those in the middle and lower sections, it did not vary significantly among the three sections ($p = 0.069$, Table 3; Fig. 4g), and no significant differences were observed in the distribution of HFOC among the *Echinochloa* biotopes, *Typha* biotopes, and bare land ($p = 0.208$, Table 3; Fig. 4c).

Table 3 ANOVA analysis of three kinds of organic carbon

	Location[a]	Biotope[b]	Location × biotope
DOC	*	***	*
LFOC	*	NA	NA
HFOC	NA	NA	NA

Locations = upper, middle, and down section of the research area

Biotopes = *Echinochloa* biotopes, *Typha* biotopes, and bare land

NA, no significant difference

*Significant difference at $p < 0.05$

**Significant difference at $p < 0.01$

***Significant difference at $p < 0.001$

DF value of the analysis: 2 for "Location," 2 for "Biotope," 4 for "Location × biotope"

F value of DOC analysis: 4.709 for "Location, " 6.814 for "Biotope," 3.368 for "Location × biotope"

F value of LFOC analysis: 4.088 for "Location," 0.4985 for "Biotope," 2.117 for "Location × biotope"

F value of HFOC analysis: 2.494 for "Location," 0.3027 for "Biotope," 0.9582 for "Location × biotope"

There were also no significant interaction terms ($p > 0.05$, Table 3). The Pearson correlation analysis showed that bulk density, vegetation dry weight, DO, water pH, and vegetation height were significantly correlated with the HFOC content (Table 4). The RDA also identified WARM as the only significant explanatory variable, although it only explained 23% of the variation in HFOC content ($p < 0.05$, Fig. 5b, Table 1).

Bacterial communities in sediment samples and their relationship with OC

More than 30 microbial phyla were identified from the subsamples, and Spearman's correlation analysis was used to identify significant correlation between microbial abundance and OC content. The results showed that Proteobacteria was the dominant phylum, and its abundance was significantly correlated with DOC, LFOC, and HFOC contents (Figs. 2 and 3). The abundances of Oxyphotobacteria, Zixibacteria, Melainabacteria, and Actinobacteria were significantly correlated with HFOC and DOC. The abundances of Spirochaetes were significantly correlated with both LFOC and DOC content. In addition, the abundances of Armatimonadetes and Cloacimonetes were significantly correlated with LFOC content. The abundances of Bacteroidetes, Firmicutes, Chloroflexi, Tenericutes, Planctomycetes, Latescibacteria, Hydrogenedentes, Synergistetes, Cyanobacteria, and Gracilibacteria were significantly correlated with DOC content.

Positive correlations were found among DOC content and the abundances of Proteobacteria, Chloroflexi, Planctomycetes, Latescibacteria, Nitrospinae, Zixibacteria, and Hydrogenedentes, while negative correlations were observed among DOC content and the abundances of Bacteroidetes, Firmicutes, Oxyphotobacteria, Acidobacteria, Tenericutes, Spirochaetes, Synergistetes, Cyanobacteria, Gracilibacteria, and Melainabacteria (Fig. 2). Proteobacteria was selected as a target microbe in our assessment of the influence of microbes on LFOC content based on its relationship with LFOC content and high relative abundance.

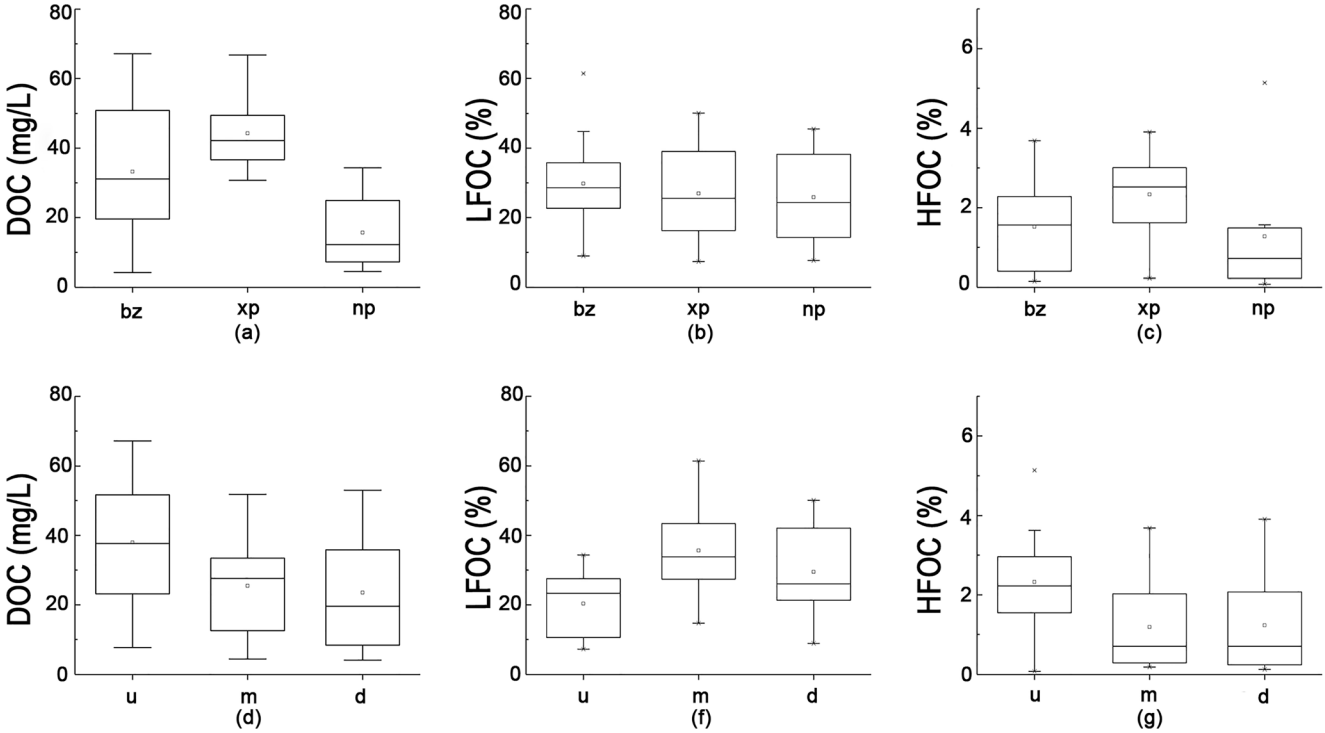

Fig. 4 The distribution of organic carbon (OC). Box plots show the distribution of OC in the river (u, m, and d represent the upper, middle, and lower sections of the research area, respectively, and bz, xp, and np represent Echinochloa biotopes, Typha biotopes, and bare land, respectively)

Proteobacteria, Oxyphotobacteria, and Actinobacteria were selected as target microbes based on their relative abundance and relationship with HFOC content (Figs. 2 and 3).

Discussion

The distribution of the three kinds of OC and their influencing factors

In our study, there were no significant differences in HFOC content among the sediments from the upper, middle, and lower sections of the river. A possible reason could be that HFOC contains only small amounts of mineralizable carbon (Alvarez and Alvarez 2000) and the mineralization of HFOC is uncommon (Alvarez and Alvarez 2000; Shahzad et al. 2018), which makes it the stable component of OC. However, we did find that HFOC contents in the middle and lower sections were lower than those in the upper section in the study. Cao et al. (2015b) reported that the distribution of HFOC varied based on sediment depth, which suggests that both the bulk density of sediments and DO influence the distribution of HFOC. Therefore, the low water level in the middle section of the river caused by dredging could explain the low HFOC content. Dredging increases the contact between sediment and air, thus increasing the air content of sediment and accelerating HFOC mineralization. In addition, dredging narrows the river and lowers the water level. Much of the sediment in the middle section of the river was sand, which poorly stored HFOC. This not only increases flow rate, and hence expedites the loss of sediment and HFOC, but also increases DO content, which can speed up the consumption of HFOC.

The LFOC consists primarily of lipids, lignin monomers, and alky-aromatics, which are larger molecules than those of DOC (Gregorich et al. 1996). Additionally, LFOC is labile, and thus can be particularly sensitive to the environmental changes, especially soil texture and pH (Liang et al. 2003). We found that DO and water pH were significantly correlated with LFOC content, and the results of the RDA also suggested that LFOC was affected by water pH, similar to the findings of Cookson et al. (2005). Marchuk et al. (2013) reported that water pH could affect the structure of the sediment by affecting the clay dispersion and ionic strength of cations, which could further affect LFOC content. Based on the results of RDA and correlation analysis, higher water pH (within the range of 7 to 8) is beneficial to the increase of LFOC, while the lipids, which consist the LFOC, are made up with fatty acids, and glycerin and the high content of hydroxyl in the alkaline environment can reduce the content of fatty acids, which lead to the decrease of LFOC. This phenomenon cannot be explained without microbes.

The DOC is an immediately available carbon source (Haynes 2000) and is more bioavailable for microbes than

Table 4 Pearson correlation analysis among organic carbon (OC) and other factors

	DOC	LFOC	HFOC	Bulk density	Sediment pH	Dry weight of plant	Water pH	Water temperature	DO	Cover degree	Plant height
DOC	1.000	0.045	0.461**	0.722***	−0.724***	0.474**	−0.072	−0.093	−0.371*	0.654*	0.668*
LFOC		1.000	0.122	0.023	−0.138	0.088	0.314*	−0.030	0.351*	0.053	0.090
HFOC			1.000	0.407*	−0.238	0.383*	−0.382*	−0.220	−0.356*	0.241	0.324*
Bulk density				1.000	−0.675***	0.388*	−0.057	0.043	−0.347*	0.349*	0.413*
Sediment pH					1.000	−0.062	−0.022	0.077	0.202	−0.407*	−0.313*
Dry weight of plant						1.000	−0.111	0.125	−0.230	0.618***	0.788***
Water pH							1.000	0.459**	0.773***	0.090	−0.039
Water temperature								1.000	0.125	0.236	0.194
DO									1.000	−0.162	−0.270
Cover degree										1.000	0.916***
Plant height											1.000

DO, dissolved oxygen; *DOC*, dissolved organic carbon; *LFOC*, light fraction organic carbon; *HFOC*, high fraction organic carbon

*Significant correlation at $p < 0.05$

**Significant correlation at $p < 0.01$

***Significant correlation at $p < 0.001$

LFOC or HFOC (Cookson et al. 2007). It mainly consists of low-molecular-weight aliphatic carboxylic acids, and macromolecular fulvic and humic acids, which are produced during the secretion and decomposition of plants, zoobenthos, and microbes (Strobel et al. 2001). Previous studies have shown that pH and the activity of microbes have significant influences on DOC (Filep et al. 2003; Filep and Rekasi 2011). Our results show that DOC content had a significantly negative correlation with sediment pH, while water pH had no effect on DOC content. This might be because DOC is held in the sediment pore water due to the viscosity of the sediments, and the DOC molecules are maintained in association with sediment particles by attractive forces (Emerson and McGarry 2003). Moreover, the increases in pH result in reductions in DOC content, mainly through the acceleration of the deprotonation of carboxylic groups (Brigante et al. 2007).

Vegetation dry weight reflects the biomass of plants growing in each biotope (Cao et al. 2017a). Our results that vegetation dry weight was significantly correlated with DOC were inconsistent with the results of the RDA. The significantly positive correlations we found between the vegetation height and DOC content were however supported by the RDA, which suggests that the size of surrounding vegetation is important in determining DOC content. The significance of vegetation height but not vegetation dry weight may be due to there being multiple sources of DOC. One of these sources is

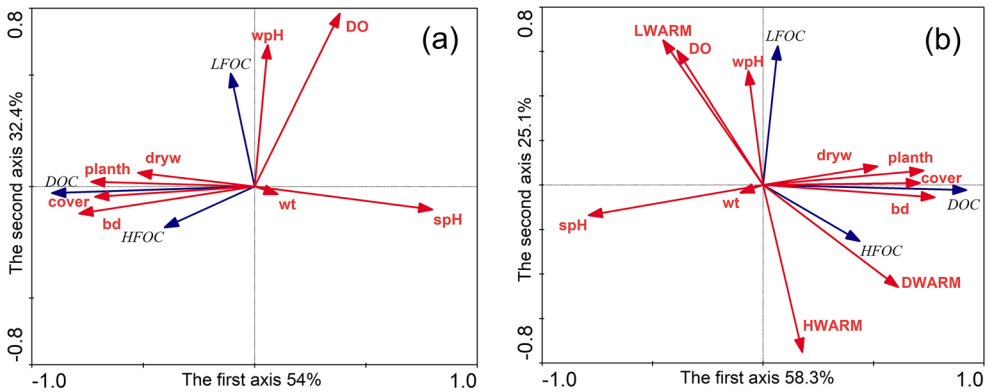

Fig. 5 The results of the redundancy analysis (RDA). Panel **a** is the result without WARM and panel **b** is the result with WARM, and the percentages on the first and second axes are the interpretations of variations. DO, dissolved oxygen; wpH, water pH; dryw, dry weight of plants; planth, vegetation height; cover, vegetation coverage; bd, bulk density; wt, water temperature; spH, sediment pH; DWARM, WARM of dissolved organic carbon (DOC); LWARM, WARM of light fraction organic carbon (LFOC); HWARM, WARM of heavy fraction organic carbon (HFOC)

the exudates generated by living plant roots (Benizri et al. 2002; Maul et al. 2013). The exudates could have been lost when plant samples were dried. The result was similar to the findings of Michel et al. (2006). Moreover, fulvic acid, which is generated by the degradation of plant bodies, can evaporate at high temperatures (Vance and David 1992). Therefore, although the RDA did not identify the dry weight of plants as an important explanatory variable, it is still likely an important factor when considering the distribution of DOC.

Proposal of a novel indicator: WARM

We propose a novel indicator to identify the correlation of all the microbes that are related to OC: WARM, based on the correlation coefficient of OC and microbes as well as the microbial relative abundance. The total correlation between OC and microbes can be quantified via this indicator, and the quantitative characteristic of WARM (i.e., magnitude, plus or minus) can reflect the strength and direction (consumption or production) of the microbial effect on OC. Moreover, WARM can also be incorporated into statistical analysis.

We found high sediment HFOC content in areas dominated by large plants and low content in bare land. This might be because plants create microhabitats in the soil, facilitating microbial growth and increasing microbial diversity (Chiarini et al. 1998). In our study, the only important factor in terms of HFOC content was WARM according to the result of RDA, which explained 23% of the variation in the distribution of HFOC. The higher levels of HFOC found in biotopes with vegetation than bare lands can be explained by the formation of large microbial aggregates related to the release of root exudates into the soil (Qin et al. 2018), which improves the bulk density of sediments and reduces DO content processes that are beneficial to carbon stabilization. The results of this study suggest that DO and sediment bulk density are the important factors in maintaining the stability of HFOC, and vegetation can facilitate the stabilization of HFOC, while the other factors primarily affect HFOC via their effects on WARM.

We only found correlations among LFOC content and the abundance of 4 microbial phyla—Proteobacteria, Spirochaetes, Armatimonadetes, and Cloacimonetes—with Proteobacteria showing a significantly negative correlation. Moreover, α-Proteobacteria, β-Proteobacteria, and γ-Proteobacteria, which had negative correlation with LFOC, were sensitive to the pH and preferred the environment with low hydrion content (Zhang et al. 2005a). We found that water pH was significantly correlated with the WARM of LFOC, indicating that water pH can affect the distribution of LFOC by modulating the abundances of microbes correlated with LFOC content. This result is inconsistent with the results of Goodwin et al. (1988). Thus, LFOC in this research exhibit positive correlation with water pH. This indicated that although WARM was eliminated as a factor influencing LFOC by RDA, WARM remained as an important indicator, since the influences of water pH and DO on the distribution of LFOC were reflected in WARM.

Based on the correlation analysis between DOC and microbial abundance, the relative abundance and the correlation coefficients of Proteobacteria, Chloroflexi, Bacteroidetes, Firmicutes, Oxyphotobacteria, Actinobacteria, and Tenericutes were selected to assess the influence of microbes on DOC content. Contrary to previous findings (Song et al. 2011), WARM was not found to be an important factor affecting the distribution of DOC. To determine the reason, we conducted correlation analysis on sediment pH, vegetation height, and WARM. The result showed that vegetation height was significantly correlated with WARM ($p = 0.003$), which was possibly the reason that WARM was excluded. The WARM was likely correlated with vegetation height due to the effects of the root exudates. Root exudates are easily utilized by microbes because they are composed by carbon-based compounds, amino acids, and other low-molecular-weight organic matter, which are also the source of DOC (Walker et al. 2003). However, when WARM was divided into positive correlation WARM (pWARM) and negative correlation WARM (nWARM), a significantly positive correlation was found between vegetation height and pWARM ($p = 0.007$), while no significant correlation was found for nWARM ($p = 0.642$). This finding suggested that the size of plants could affect the DOC content by affecting the related microbes that were positively associated with DOC content. A significant correlation between nWARM and DOC was also found, while nWARM was not correlated with plant height, suggesting that these microbes utilized other sources of DOC. Among the microbes negatively correlated with DOC, Actinobacteria is the main plant residue decomposer (Ventura et al. 2007), suggesting that decomposing vegetation is more important for these microbes than root exudates. Overall, these results indicated that the microbes whose abundance was positively correlated with DOC content relied on different DOC sources relative to those whose abundance was negatively correlated with DOC content. Positively correlated microbes may favor plant-derived DOC (Stepanauskas et al. 2000), which is produced by living plants. In contrast, negatively correlated microbes may favor DOC produced by the degradation of residual bodies (Clay et al. 2009). These interactions may also explain why DOC content was lower in *Echinochloa* biotopes than in *Typha* biotopes. This study confirms that sediment pH and vegetation height are important factors affecting the distribution of DOC in wetlands.

We found that WARM is a useful indicator in examining the influence of microbes over the distribution of OC. By dividing WARM into pWARM and nWARM, potential sources of DOC can be revealed. While the spatial and temporal resolutions of our study might limit the extrapolation of our conclusions to all the wetland areas, we believe that our

work is important in the context of riverine wetlands with similar conditions. In addition, WARM is a reasonable and effective indicator that can be used to study the influence of microbes on OC in wetlands.

Conclusions

In this study, the distribution of OC in riverine wetlands was researched and the different distribution patterns of three kinds of OC were revealed. The content of HFOC was higher in river environment dominated by large plants. LFOC was not sensitive to the presence of plants and the size of plants. DOC varied significantly, and high concentration appeared in the biotopes dominated by large plants (*Typha*). Moreover, the distribution and concentration of OC were found to be affected by both environmental factors and microbial communities. In our study, DOC was significantly affected by sediment pH rather than water pH, while water pH was an important environmental factor controlling the distribution of LFOC. The DO and physicochemical characters of HFOC were the most important factors that affected the distribution of HFOC. Microbial communities played a critical role in the distribution of OC though their direct and indirect influencing mechanisms. The indicator WARM was proposed to objectively reflect the relative abundance of microbes and the composition of microbial communities. Our study revealed the environmental factors that affect the distribution of OC in riverine wetlands and, for the first time, suggests that WARM is an effective and objective indicator to study the relationship between OC and microbial communities.

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