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WETLANDS RESTORATION

Soil Organic Carbon and Nitrogen Variations with Vegetation Succession in Passively Restored Freshwater Wetlands

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Abstract

Passive restoration after agricultural abandonment has been widely practiced to improve soil quality and recover the ecological functions of degraded wetlands. However, studies concerning the relationships between soil and vegetation during natural succession are still lacking. In this study, the variations of soil organic carbon (SOC) and total nitrogen (TN), as well as their relationships with soil and vegetation properties were evaluated in passively restored freshwater wetlands with a chronosequence (2, 4, 8, 13, 16, and 20 years) on the Sanjiang Plain, China. An adjacent natural wetland was chosen as a reference system. Results indicated that soil and vegetation in restored wetlands changed substantially overtime, and gradually came to resemble natural wetlands. SOC and TN contents in the 10–30 cm soil layers required less time to achieve a natural level than those in the 0–10 cm soil layers. They were significantly correlated with soil water content and conductivity, especially in the 0–10 cm layer. Moreover, SOC and TN storages were synergistically improved, and highly dependent on plant diversity, height, coverage, and biomass. These results suggest that passive restoration is an efficient measure for forming wetland plant communities after agricultural abandonment, and ultimately enhances SOC and TN accumulation in restored wetlands.

Keywords Natural succession · Passive restoration · Soil organic carbon · Soil total nitrogen · Wetland function

Abbreviations

AGB	aboveground biomass
BGB	belowground biomass
IV	important value
SBD	soil bulk density
SC	soil conductivity
SOC	soil organic carbon
SWC	soil water content
TN	total nitrogen
TSN	total soil nitrogen storage
TSOC	total soil organic carbon storage

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Introduction

More than half of the world's natural wetlands have been lost because of intensified anthropogenic disturbance (Mitsch and Gosselink 2007). Agricultural reclamation is considered to be the main cause of wetland loss (Yu et al. 2017). The resulting changes in soil and vegetation conditions also contribute to the degradation of wetland functions (Robertson and James 2007). Ecological restoration of damaged and degraded wetlands via adaptive management is needed to restore wetland functions (Ballantine et al. 2012). Agricultural abandonment of reclaimed freshwater wetlands (passive restoration), driven by policy and socioeconomic changes, is seen as an efficient measure for wetland restoration in inland areas (Inglett and Inglett 2013; An et al. 2018). Wetland restoration has an important impact on several ecological processes of key components (e.g., soil, vegetation), and improves ecosystem structure and function toward a reference ecosystem (Ballantine et al. 2012). The re-establishment of ecological functions in restored wetlands is always associated with soil properties, including soil nutrient accumulation and cycling (Zhang et al. 2007). Monitoring soil nutrient dynamics after the restoration has been initiated which can provide basic data for evaluating the development of ecosystem functions and restoration processes (Ballantine and Schneider 2009). Therefore, detailed investigation of changes to soil nutrients in passively restored wetlands during natural succession is essential.

The re-establishment of plant communities can directly reflect the ecological processes of restored freshwater wetlands (Sutton-Grier et al. 2013). Specifically, species diversity, coverage and biomass in plant communities are widely employed as indicators for evaluating the effects of restoration practices (Jin 2008; Ballantine and Schneider 2009). Therefore, the vegetation has an important role in restoration targets for freshwater wetlands, and its changes during ecosystem succession need to be investigated. In addition, wetland vegetation significantly influences the nutrient content in the surface soil through nutrient absorption and reallocation (Gathumbi et al. 2005; Christensen and Crumpton 2010), and consequently regulates the biogeochemical cycles in ecosystems (Bormann and Sidle 1990). There is evidence that soil carbon and nitrogen are linked with vegetation succession in restored grassland ecosystems (Deng et al. 2013; Li et al. 2014). Research has focused on the success of restored coastal wetlands in terms of plant biodiversity, plant cover, biomass production, and soil properties, as well as their interactions (Craft et al. 1999; Craft et al. 2002; Cui et al. 2009); however, less is known about the potentially critical impact of vegetation changes on soil nutrient status in restored freshwater wetlands.

There is increasing attention on how freshwater wetland restoration affects the soil processes including soil organic matter, nitrogen, and other properties (Hogan et al. 2004; Ballantine and Schneider 2009; Ballantine et al. 2012; Sutton-Grier et al. 2013). It is reported that the passive restoration after agricultural abandonment can effectively increase soil organic carbon (SOC) and total nitrogen (TN) with longer successional age (Inglett and Inglett 2013); vegetation provides the main organic matter input to wetland soil (Anderson et al. 2005). The biological condition of wetlands has feedback effects on the physicochemical environment (Wang et al. 2014). Changes in plant community composition can influence the input of soil organic matter and other nutrients in freshwater wetlands through specific plant-soil feedbacks (Sutton-Grier et al. 2013). Conversely, the soil nutrient availability, pH, and other physicochemical properties can affect the distribution and diversity of plant communities (Christensen and Crumpton 2010). Thus, the plant-soil feedback depends on both vegetation type and specific differences in soil condition. Understanding the effects of plant-soil interactions on ecological functions during successional processes is essential for the assessment of soil and plant synergies in restored wetlands.

The formation of SOC during natural succession is mainly derived from the plants in the restored wetland ecosystem (Wang et al. 2015). Given that plant species have dissimilar effects on nutrient accumulation, higher plant diversity is necessary for improving the multi-functionality of restored wetlands (Sutton-Grier et al. 2013). Studies have found that, even after 11–20 years, the soil carbon and nitrogen in restored wetlands restored for 11–20 years is lower than that in natural wetlands (Yu et al. 2017). Examining the dynamics of SOC and TN, and their determinants in passively restored freshwater wetlands after agricultural abandonment is vital to achieve the goal of fully restored wetlands. We hypothesize that, after passive restoration, the contents of SOC and TN will change profoundly, and reach the level of natural wetlands at a certain successional stage. Also, we hypothesize that soil carbon and nitrogen accumulation in restored wetlands is determined not only by soil attributes but also by vegetative changes. Here, a study was conducted on restored freshwater wetlands with a chronosequence of agricultural abandonment on the Sanjiang Plain, China. The specific objectives of this study were (1) to investigate the changes in vegetation across restoration ages, (2) to compare the SOC and TN contents in restored and natural wetlands, and (3) to ascertain the relationships between the accumulations of SOC and TN, and soil and vegetation properties. The results of this study will improve our knowledge of plant community succession and restoration of ecosystem function.

Material and Methods

Site Description

The study area is located in Honghe farmland (47°27′-47°46′ N, 133°19′-133°40′E) and Honghe National Nature Reserve (HNNR) (47°43′-47°52′N, 133°37′-133°45′E) on the Sanjiang Plain, China. The region has a temperate humid and semi-humid continental monsoon climate. The annual average temperature is 1.9 °C, and the annual average rainfall is about 600 mm. Around 70% of the annual rainfall falls during June to September. The main soil types in this area are meadow soil and marsh soil. The vegetation types here are meadow and wetland plants.

During the past five decades, many freshwater wetlands in the Honghe farmland were extensively reclaimed for agriculture to supplement the food supply for the growing population, resulting in serious loss and degradation of natural wetlands in this region. Agricultural abandonment of reclaimed wetlands has become the major method for wetland restoration. In the past two decades, many agricultural fields have consequently been abandoned for passive restoration. As a result, the area of passively restored wetlands has started to increase rapidly.

A number of former *Calamagrostis angustifolia* wetlands undergoing passive restoration have been established in Honghe farmland and HNNR. In this study, we selected seven wetland sites including six restored sites with a chronosequence and one natural site. The six restored sites have been passively restored for different lengths of time: 2 years (2Y, agricultural abandonment since 2014), 4 years (4Y, agricultural abandonment since 2012), 8 years (8Y, agricultural abandonment since 2008), 13 years (13Y, agricultural abandonment since 2003), 16 years (16Y, agricultural abandonment since 2000), and 20 years (20Y, agricultural abandonment since 1996). Before reclamation, all the restored sites were typical *C. angustifolia* wetlands located in the Nongjiang River Basin (Fig. 1) which had been cultivated since the 1980s. After reclamation, the main cropping practice was corn-soybean rotation. In addition, we used a natural *C. angustifolia* wetland (ND, non-degraded) to represent the reference system. All the restored and natural wetland sites were in close proximity and had similar environmental conditions. Hydrological conditions in this area are mainly regulated by groundwater connections to the Nongjiang River and Bielahong River, precipitation, and evapotranspiration.

Field Surveys and Sampling

Field surveys were carried out using transect and quadrat methods in August 2016. We established three equal-sized transects (50 m length × 10 m width) in each restored wetland site and the natural wetland site. Three quadrats (1 m × 1 m) were randomly set within each transect (9 quadrats in each

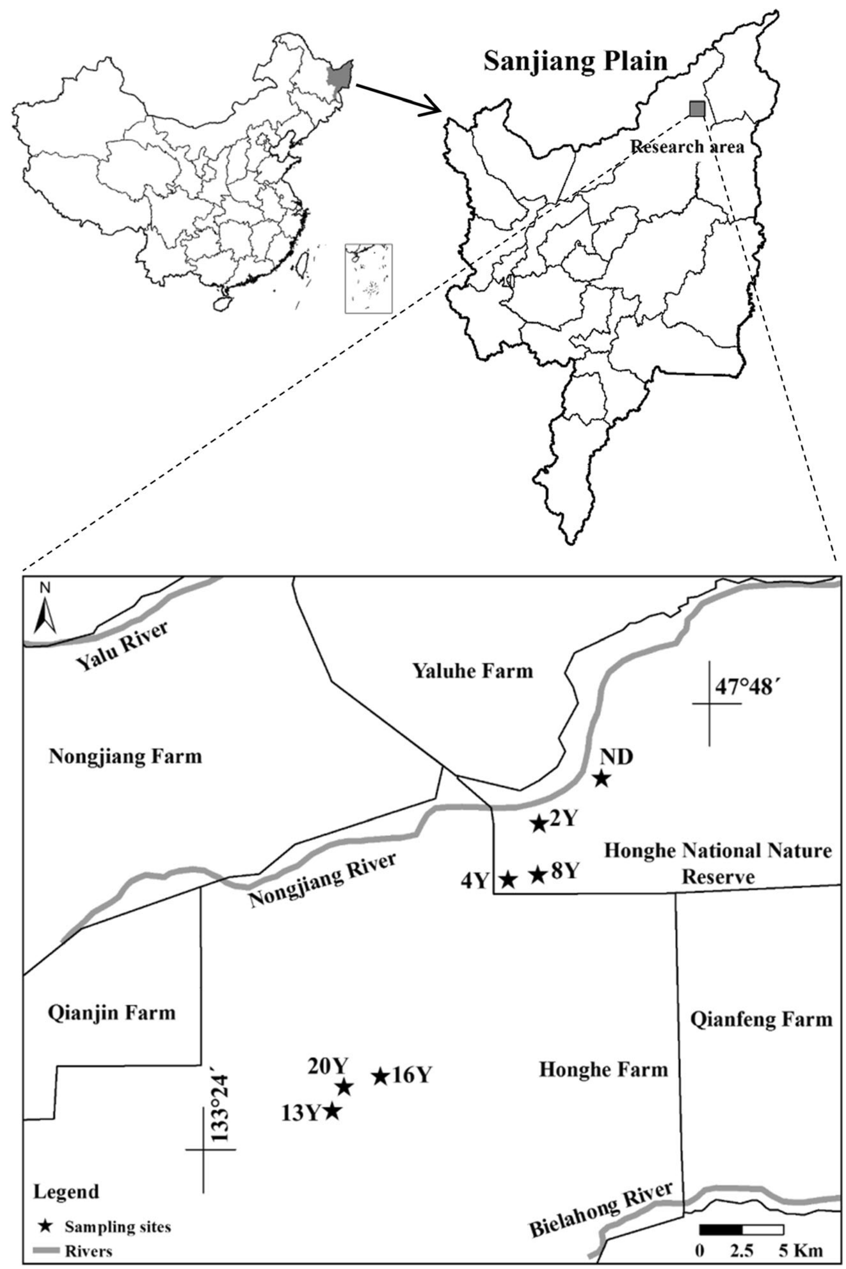

Fig. 1 Location of research area and sampling sites in this study. Site ages used are years since agricultural abandonment at the time of sampling: 2Y, 2-year restored wetlands; 4Y, 4-year restored wetlands; 8Y, 8-year restored wetlands; 13Y, 13-year restored wetlands; 16Y, 16-year restored wetlands; 20Y, 20-year restored wetlands; ND, non-degraded wetlands

wetland site). All the plant species in each quadrat were recorded. The plant height was measured, and the plant density was determined by counting the number of live plants within quadrats. The coverage was estimated as the ratio of the vertical projection of exposed leaf area to the area of each quadrat. All the aboveground parts were removed at the ground level, and then oven dried at 65 °C for 72 h to measure aboveground biomass (AGB).

To measure the belowground biomass (BGB), a subquadrat (25 cm × 25 cm) was set within each quadrat, and excavated to 30 cm soil depth. The soil samples were air-dried and crushed to pass through a 2-mm sieve to isolate the majority of plant roots. Fine roots remaining in the soil were further isolated by spreading soil in shallow trays and filling the trays with distilled water. The outflow from the trays passed through a mesh sieve of 0.5 mm. All of the belowground parts were then oven-dried at 65 °C for 72 h and weighed.

To measure the soil water content (SWC), a soil auger (5 cm in diameter) was used to collect three samples within each quadrat. Soil samples were separated into layers of 0–10 cm, 10–20 cm, and 20–30 cm depths, oven-dried at 105 ± 2 °C for at least 72 h, and then weighed. Soil bulk density (SBD) was measured in the field using a stainless-steel cylinder (volume of 100 cm^3) (Wu et al. 2010). To measure soil pH, conductivity (SC), SOC, and TN, another three soil cores were taken within each quadrat. The soil was separated into 0–10 cm, 10–20 cm, and 20–30 cm layers. The samples from the same soil layer within each quadrat were combined to give one sample per quadrat for each soil depth to reduce heterogeneity within the quadrat. The mixed soil from each layer was then divided into three sub-samples to measure SC, SOC, and TN. The soil samples were placed in polyethylene bags, and then air-dried in the laboratory. All the soil samples were ground and sieved (mesh size, 2 mm) for physicochemical analysis.

Laboratory Analysis

The pH of soil was determined using a pH meter (Tes-1381 k, Taiwan) in a 1:5 soil/water suspension. Afterward, SC was determined using a conductivity meter (AZ86503, Taiwan). SOC content was determined by KCr_2O_7+H_2SO_4 digestion and $FeSO_4$ titration method (Niu et al. 2011). TN was determined using a fully automatic chemical analyzer (Smartchem 300, Italy).

Data Analyses

To determine the variations in plant communities among the restored and natural wetlands, the important value (*IV*) of each plant species was calculated using the following formula (Na et al. 2018):

$$IV = (RF + RD + RH + RC)/4$$

where: *RF* is the relative frequency; *RD* is the relative density; *RH* is the relative plant height; and *RC* is the relative coverage.

The Shannon-Wiener diversity index (*H*), richness index (*R*), and evenness index (*E*) were calculated using the following formulas:

Shannon-Wiener diversity index $(H) = -\sum_{i=1}^{s} P_i \ln P_i$.

Richness index $(R) = (S\text{-}1)/\ln N$

Evenness index $(E) = H/\ln S$

where: P_i is the important valve of plant species *i*; *S* is the number of total plant species observed in each community; and *N* is the sum of plant individuals.

The total soil organic carbon storage (TSOC; $kg \cdot m^{-2}$) and total soil nitrogen storage (TSN; $kg \cdot m^{-2}$) were calculated using following formulas described by Li et al. (2014):

$$\text{TSOC} = \sum D_i \times B_i \times SOC_i$$
$$\text{TSN} = \sum D_i \times B_i \times TN_i$$

where D_i, B_i, SOC_i, and TN_i are the soil thickness (m), bulk density (g cm^{-3}), soil organic carbon content (g kg^{-1}), and total nitrogen content (g kg^{-1}) in soil layer *i*, respectively.

One-way analysis of variance (ANOVA), followed by the least significant difference (LSD) multiple comparison test, was performed to compare the vegetation and soil properties among different wetland sites. Differences were considered significant when $P < 0.05$. Pearson's correlation analysis was performed to determine the relationships between the accumulation of soil carbon and nitrogen, and soil and vegetation properties. Prior to correlation analysis, the data were checked for normal distribution with a Kolmogorov–Smirnov test. Logarithmic transformations were performed on the variables that were not normally distributed. The coefficient (*r*) at $P < 0.05$, $P < 0.01$, and $P < 0.001$ levels was used to check for significant correlations. All the statistical analyses were carried out in SPSS 18 (IBM Inc., Chicago, IL, USA).

Results

Variations of Vegetation and Soil Physical Properties

The dominant species differed among the seven freshwater wetland sites (Table 1). At the early stage of natural succession, the ruderal weed *Artemisia argyi* was the dominant species in the 2Y site, and *Calamagrostis brachytricha* was the dominant species in the 4Y site. The plant community in the 8Y site was dominated by the sedges *Carex appendiculata.* The *IV* of *C. angustifolia* increased with restoration age, and this plant became the dominant species when wetlands had been restored for 16 years. In the 20Y site, *C. angustifolia* had the highest *IV* value (48.89), followed by other sedges *C. appendiculata* and *C. lasiocarpa*.

Table 1 The vegetation properties in the different wetland sites

Wetland sites	Dominant species (*IV*)	*H*	*R*	*E*	Height (cm)	Coverage (%)	Density (No. m^{-2})	AGB (g m^{-2})	BGB (g m^{-2})
2Y	*Artemisia argyi* (15.92), *Phragmites australis* (11.54), *Calamagrostis brachytricha* (10.22)	2.76e	2.40 g	0.89e	30.8a	44.1a	1885d	195.2b	157.9a
4Y	*C. brachytricha* (19.06), *A. argyi* (14.08), *P. australis* (11.32)	2.59d	2.30f	0.88e	52.0b	64.0b	1354c	159.1ab	629.2b
8Y	*Carex appendiculata* (24.03), *C. angustifolia* (19.96), *C. lasiocarpa* (11.10)	2.38c	2.104e	0.84d	51.0b	75.5c	1026b	114.5a	810.6b
13Y	*C. angustifolia* (31.32), *C. appendiculata* (16.42), *P. australis* (8.09)	2.28c	1.90d	0.82 cd	50.8b	76.0c	803a	150.8ab	1149.4c
16Y	*C. angustifolia* (31.40), *C. appendiculata* (23.63), *C. lasiocarpa* (8.22)	2.09b	1.62c	0.79c	71.4c	86.8d	639a	246.4c	1901.6d
20Y	*C. angustifolia* (48.89), *C. appendiculata* (10.31), *C. lasiocarpa* (8.20)	1.82a	1.50b	0.70a	94.8d	95.9e	631a	422 .0e	3398.6f
ND	*C. angustifolia* (46.96), *C. lasiocarpa* (11.88), *C. appendiculata* (10.22)	1.73a	1.15a	0.75b	90.8d	90.7de	801a	300.9d	2911.6e

Notes: Abbreviations are 2Y, 2-year restored wetlands; 4Y, 4-year restored wetlands; 8Y, 8-year restored wetlands; 13Y, 13-year restored wetlands; 16Y, 16-year restored wetlands; 20Y, 20-year restored wetlands; ND, non-degraded wetlands; *IV*, important value; *H*, Shannon-wiener index; *R*, Richness index; *E*, Evenness index; AGB, aboveground biomass; BGB, belowground biomass. Data is mean (n=9). Different letters in the same column indicate significant difference at $P < 0.05$

Results showed that plant species diversity, richness, and evenness in restored sites decreased with restoration age, being highest in the 2Y site than in older sites (Table 1). The plant species diversity in the 20Y site closely approached that in the ND site, although there were significant differences in richness and evenness indices between the two sites. Plant height and coverage were the lowest in the 2Y site ($P <$ 0.05), and highest in the 20Y and ND sites (Table 1). In contrast, plant density was highest in the 2Y site, and it generally decreased with restoration age. AGB decreased from 2 to 13 years, and then increased with age. Unlike AGB, BGB increased with restoration age, and reached the highest value in the 20Y site. AGB and BGB in the 20Y site were 422 .0 g m^{-2} and 3398.6 g m^{-2}, being higher than those in the ND site.

The SWC in restored wetland sites generally increased with restoration age (Table 2). There was no significant difference in SWC in the 0–20 cm soil layer between the 20Y site and ND site. In addition, SWC decreased with soil depth. SBD was relatively higher in 2Y site, and changed slightly with restoration ages. It was generally higher in the deeper soil layer than that in surface soil layer across experimental sites. Soil pH was higher in the 20–30 cm soil layer than that in other soil layers, and it increased with restoration age. The 2Y site had highest SC, whereas the ND site had the lowest level. Similar to the variations of SBD and pH, higher SC was observed in the 20–30 cm soil layer.

Vertical Changes in SOC and TN Contents

The SOC and TN contents varied among the three soil layers ($P < 0.05$; Fig. 2). Both SOC and TN contents were higher in the 0–10 cm soil layer than in the other layers, and generally increased with restoration age. The SOC content of the 0–10 cm soil layer in the 20Y site was 37.3 g kg^{-1}, and it was similar to that in the ND site ($P > 0.05$; Fig. 2a). In the 10–20 cm and 20–30 cm soil layers, SOC contents in the 8Y site reached the level of the ND site. There was no significant difference in TN contents in the 0–10 cm soil layer between the 16Y site and ND site. The TN content of the 0–10 cm soil layer in the 20Y site was 3.9 g kg^{-1}, and it was significantly higher than that in the ND site ($P < 0.05$). In the 10–20 cm and 20–30 cm soil layers of the 13Y site, TN contents achieved the level of the ND site (Fig. 2b). They were higher in the 16Y and 20Y sites than that in the ND site.

Relationships between SOC and TN Contents and Soil and Vegetation Properties

Correlation analysis showed that SOC and TN contents were positively correlated with SWC in the 0–10 cm soil layer, whereas they were negatively correlated with SC in the 0–10 cm and 20–30 cm soil layers ($P < 0.05$; Table 3). The SOC content in the 0–10 cm soil layer and the TN content in the 20–30 cm soil layer were positively correlated with soil pH ($P < 0.05$). SOC and TN contents, especially in the 0–10 cm soil layer, were negatively correlated with diversity, richness, and evenness. Both SOC and TN contents across the 0–30 cm soil layers were positively correlated with coverage, whereas they were negatively correlated with plant density ($P < 0.05$). Also, they were positively correlated with plant height, with the exception of SOC content in the 20–30 cm soil layer. There was a positive correlation between TN content in the 0–10 cm soil layer and AGB. In addition, the

Table 2 Soil physical properties in the different wetland sites

Wetland sites	SWC (%)			SBD (g cm^{-3})			pH			SC (μs cm^{-1})		
	0–10 cm	10–20 cm	20–30 cm	0–10 cm	10–20 cm	20–30 cm	0–10 cm	10–20 cm	20–30 cm	0–10 cm	10–20 cm	20–30 cm
2Y	33.35a	31.71a	26.42a	1.14b	1.22ab	1.49c	6.49a	6.50a	6.87a	147.10c	170.18 cd	258.06c
4Y	37.25a	39.26a	35.26ab	0.94ab	1.03ab	1.19ab	6.60ab	6.48a	6.86a	135.00c	219.24d	251.31c
8Y	58.75b	38.94a	37.34b	0.84a	0.98ab	1.26ab	6.54a	6.70ab	7.04ab	93.07b	124.21bc	182.31b
13Y	57.66b	47.80ab	34.73ab	0.91ab	0.91a	1.06a	6.58ab	6.72ab	6.97ab	52.30a	78.29ab	122.13a
16Y	55.03b	44.33a	39.37b	0.78a	1.05ab	1.30bc	6.73ab	7.04bc	7.22bc	50.09a	75.13ab	99.04a
20Y	61.44b	50.70ab	39.99b	0.99ab	1.33b	1.21ab	6.89b	7.07bc	7.29bc	57.43a	66.70ab	91.74a
ND	62.32b	64.17b	53.89c	0.83a	1.03ab	1.32bc	7.21c	7.42c	7.50c	53.56a	58.30a	63.37a

Notes: Abbreviations are 2Y, 2-year restored wetlands; 4Y, 4-year restored wetlands; 8Y, 8-year restored wetlands; 13Y, 13-year restored wetlands; 16Y, 16-year restored wetlands; 20Y, 20-year restored wetlands; ND, non-degraded wetlands; SWC, soil water content; SBD, soil bulk density; SC, soil conductivity. Data is mean (n=9). Different letters in the same column indicate significant difference at $P < 0.05$

TN contents of the three soil layers were positively correlated with BGB, and SOC content was positively correlated with BGB ($P < 0.05$).

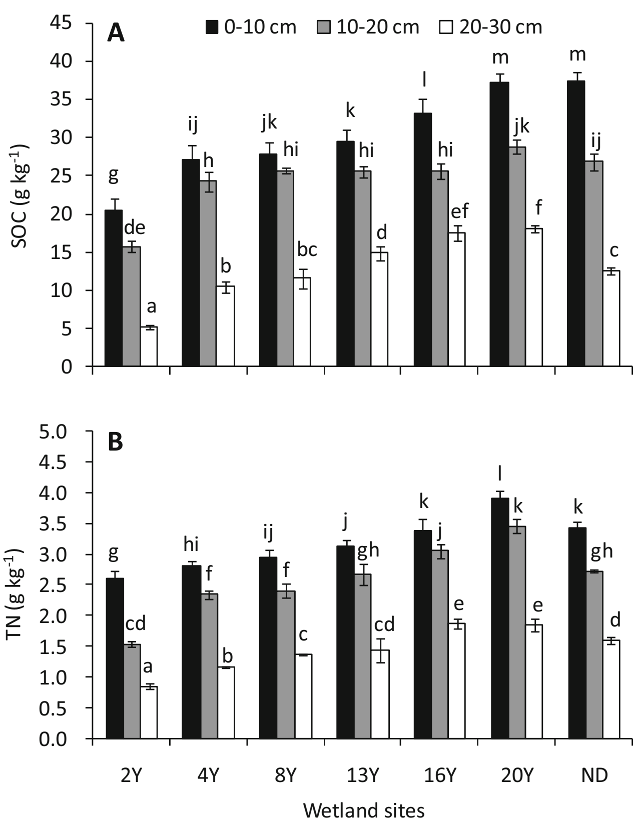

Fig. 2 Vertical changes in soil organic carbon (SOC) (**a**) and total nitrogen (TN) (**b**) contents in different wetland sites. Abbreviations are 2Y, 2-year restored wetlands; 4Y, 4-year restored wetlands; 8Y, 8-year restored wetlands; 13Y, 13-year restored wetlands; 16Y, 16-year restored wetlands; 20Y, 20-year restored wetlands; ND, non-degraded wetlands. Different letters above the bars indicate significant differences at $P <$ 0.05 level

Relationships between TSOC and TSN and Soil and Vegetation Properties

Results showed a significant correlation between TSOC and TSN ($P < 0.01$; Table 4). TSOC and TSN were positively correlated with SWC ($P < 0.01$), whereas TSOC was negatively correlated with SBD ($P < 0.05$). Both TSOC and TSN were negatively correlated with SC ($P < 0.01$). There was no significant relationship between TSOC and TSN and pH ($P >$ 0.05).

TSOC was significantly correlated with diversity, richness, and evenness ($P < 0.05$; Table 5), and TSN was negatively correlated with diversity and evenness ($P < 0.05$). TSOC and TSN were positively correlated with plant height and coverage ($P < 0.05$), whereas TSOC was negatively correlated with plant density ($P < 0.05$). Both TSOC and TSN were positively correlated with AGB and BGB ($P < 0.05$).

Discussion

In this study, the plant community at earlier stages of passive restoration was mainly dominated by weeds remaining from farmlands, and the plant diversity was relatively higher. With natural succession, the vegetation was gradually dominated by meadow and wetland plants that existed in natural wetlands. These results agree with related research that shows that perennial plants gradually dominate and expand in restored freshwater wetlands (Wang et al. 2019). The decline in plant species diversity in older restored communities may be explained by the fact that biological filtration helps restore the diversity of ecosystems by eliminating agricultural weeds (An et al. 2018). The development of dominant species, such as *C. angustifolia* and *Carex* spp. in older restored wetlands enhances their competitiveness, and ultimately results in an

Table 3 Pearson's correlation coefficients (*r*) between SOC and TN contents in different soil depths and the properties of soil and vegetation

Soil depth		Soil physical properties				Vegetation properties							
		SWC	SBD	pH	SC	*H*	*R*	*E*	Height	Coverage	Density	AGB	BGB
0–10 cm	SOC	0.825*	−0.579	0.853*	−0.843*	−0.980***	−0.945***	−0.937**	0.977***	0.970***	−0.887**	0.728	0.957**
	TN	0.780*	−0.362	0.707	−0.815*	−0.924**	−0.855*	−0.985***	0.936**	0.926**	−0.8528*	0.847*	0.965***
10–20 cm	SOC	0.698	−0.166	0.622	−0.602	−0.796*	−0.704	−0.759*	0.798*	0.932**	−0.918**	0.417	0.743
	TN	0.631	0.120	0.665	−0.704	−0.835*	−0.749	−0.876**	0.856*	0.944***	−0.937**	0.653	0.846*
20–30 cm	SOC	0.456	−0.587	0.563	−0.798*	−0.748	−0.674	−0.785*	0.732	0.891**	−0.949***	0.520	0.732
	TN	0.634	−0.379	0.763*	−0.887**	−0.870*	−0.820*	−0.870*	0.850*	0.955***	−0.956***	0.618	0.839*

Notes: Abbreviations are SOC, soil organic carbon; TN, total nitrogen. SWC, soil water content; SBD, soil bulk density; SC, soil conductivity. *H*, Shannon-wiener index; *R*, Richness index; *E*, Evenness index; AGB, aboveground biomass; BGB, belowground biomass. *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$

overall decrease in species density and diversity. The similarity index of vegetation characteristics between restored wetlands and the reference system gradually increased with restoration age (Meyer et al. 2008; Guo et al. 2017; An et al. 2018). However, previous studies indicate that it is difficult to restore the vegetation of abandoned agricultural fields to the original level even when wetlands have been passively restored for more than a decade (Mulhouse and Galatowitsch 2003; Stroh et al. 2012).

Soil processes are particularly important because physical and chemical properties are directly linked to the development of freshwater wetland functions (Ballantine and Schneider 2009). In this study, the soil physical properties in 20-year restored wetlands generally had reached the level of natural wetlands. In particular, the SWC in restored sites was consistent with another study finding that soil moisture could effectively recover after passive restoration for more than 20 years (An et al. 2019). The generally consistent SBD among the restored and natural wetlands suggests that the SBD may be an insensitive indicator for assessing passive restoration in this area. The soil pH in the restored sites was lower and EC was higher than that in natural wetlands, which could be because of fertilization during the former agricultural production (Wang et al. 2015). Other studies found that soil quality in wetlands develops with restoration age, and gradually becomes equivalent to the levels of natural wetlands (Craft et al. 2002). In terms of soil nutrients,

Table 4 Pearson's correlation coefficients (*r*) between TSOC and TSN and soil properties

	TSN	SWC	SBD	pH	SC
TSOC	0.943**	0.651**	−0.473*	0.006	−0.689**
TSN	1	0.571**	−0.260	0.046	−0.641**

Notes: Abbreviations are TSOC, total soil organic carbon storage; TSN, total soil nitrogen storage; SWC, soil water content; SBD, soil bulk density; SC, soil conductivity. ** $P < 0.01$, * $P < 0.05$

the surface soil (0–10 cm) had higher contents of SOC and TN than the deeper soil layer (10–30 cm) in the restored wetlands and reference system, suggesting that the 0–10 cm soil layer has a greater potential for carbon and nitrogen sequestration. This is probably explained by the slower decomposition rate in anaerobic conditions and the lower accumulation of soil organic matter in deeper soil. Also, the absence of electron acceptors such as iron oxides and hydroxides under reducing conditions in deeper soil may slow down organic matter oxidation and mineralization (Sahrawat 2003).

The development of soil in restored freshwater wetlands is considered a relatively slow process, which commonly appears to accelerate in later successional phases (Zedler and Callaway 1999; Ballantine and Schneider 2009). Changes in the soil nutrient status commonly associated with the recovery sequence may directly influence soil development. However, a study has shown that natural restoration, after a certain period of time, does not necessarily promote SOC and nitrogen in degraded wetlands to the original level (Hossler and Bouchard 2010). The results in our study demonstrated that the SOC content in the restored soils developed and gradually approached the level in natural wetlands with time since restoration (e.g., the 0–10 cm soil layer in the 20Y restored site, and the 10–30 cm soil layer in the 8Y restored site), supporting the first hypothesis of this study. Similar to previous research showed that degraded wetlands required 7–20 years of restoration to develop SOC and organic matter conditions (Card et al. 2010; Wolf et al. 2011). In this study, the TN content in the surface soil layer (0–10 cm) of restored wetlands began to reach a natural level after 16 years' restoration, while TN in deeper soil layer needed a 13-year period, thus also supporting our first hypothesis. A relevant study demonstrated that the recovery of nitrogen was faster than other nutrients (Inglett and Inglett 2013), explaining our finding that the nitrogen content in the surface soil layer (0–10 cm) in restored wetlands took a shorter time to reach the level of natural wetlands than organic carbon.

Table 5 Pearson's correlation coefficients (r) between TSOC and TSN and vegetation properties

	H	R	E	Height	Coverage	Density	AGB	BGB
TSOC	−0.854*	−0.759*	−0.943**	0.917**	0.891**	−0.806*	0.848*	0.929**
TSN	−0.781*	−0.692	−0.917**	0.854*	0.787*	−0.691	0.914**	0.895**

Notes: Abbreviations are TSOC, total soil organic carbon storage; TSN, total soil nitrogen storage; H, Shannon-wiener index; R, Richness index; E, Evenness index; AGB, aboveground biomass; BGB, belowground biomass. ** $P < 0.01$, * $P < 0.05$

The results in this study show that SOC and TN in restored wetlands have similar trends along successional age. In this case, the coupling effect between carbon and nitrogen cycles is strong. The high and positive correlation between SOC and TN was also found in a previous study (Bai et al. 2010). Moreover, the sequestration of organic carbon in the soil after agricultural abandonment was greatly influenced by nitrogen accumulation (Knops and Tilman 2000), helping to explain the close relationship between SOC and TN in this study. Carbon and nitrogen interactions are crucial to determine whether the carbon sink can be maintained in terrestrial ecosystems after long-term succession (Luo et al. 2006). This study also found close relationships between soil physical properties and SOC and TN, especially in the 0–10 cm soil layer, supporting our second hypothesis. Significant correlations between carbon and nitrogen storages and SWC can possibly be attributed to the promotion of vegetation development through hydrological recovery which affects the organic matter accumulation of wetlands (Price and Waddington 2000). However, significant negative correlations between the accumulations of SOC and TN, and soil conductivity were detected in this study, implying that salt ions inhibit soil carbon sequestration. This is supported by a past research showing close relationships between soil conductivity and nutrients (Wang et al. 2015).

The evolution of soil properties has potential effects on the plant community composition and structure (Kardol et al. 2006). Conversely, vegetation succession determines the carbon and nitrogen storages in the soil to a certain extent (Wu et al. 2010). The interactions between plants and soil were also found in this study. The SOC and TN accumulations are closely related to vegetation properties, further supporting the second hypothesis of this study. There are a series of potential interaction mechanisms to explain the synergistic development of SOC and TN. After agricultural abandonment, the rapid development of vegetation and increased biomass production result in an elevated input from plant litter, thereby, increasing the soil carbon and nitrogen content (Callaway et al. 2003; Ballantine and Schneider 2009). This means that the primary productivity of plants is a key factor controlling soil nutrient accumulation. In particular, the increase in BGB along successional ages, as well as the dead roots and root exudates also contributed to soil carbon and nitrogen sequestration (Dijkstra et al. 2013). The results of this study further demonstrate that carbon and nitrogen contents across the three soil layers are strongly correlated with BGB but weakly correlated with AGB. The greater contribution to SOC and TN derived from belowground biomass is related to increasing production and residue input, especially in the 10–20 cm soil layer where the roots are mainly distributed. This further explains why carbon and nitrogen contents in deeper soil needed less time to reach the natural level than that in surface soil in this study.

The changes in soil nutrients may reflect the shifts in plant community composition and diversity (Ehrenfeld 2001). There were strong correlations between TSOC and TSN and plant diversity in this study, indicating that plant diversity had significant effects on nutrient accumulation in restored wetlands undergoing natural succession. This is possibly due to the multiple interrelated processes and complex plant-soil feedbacks (Chen et al. 2018). The results of this study are consistent with the relationships between soil carbon and nitrogen with species richness that were found previously in a natural wetland ecosystem (Wu et al. 2013). Species-specific effects can explain this result, as soil nutrients readily accumulate in wetlands restored with certain species (Callaway et al. 2003; Means et al. 2016). In this study, the formation of SOC and TN in restored wetlands was most likely derived from associated plants such as *Carex* spp., and *C. angustifolia*, which have high potential to accumulate carbon and nitrogen. Therefore, the plant species diversity emerges as a significant predictor for SOC and TN storages in restored wetlands.

Conclusions

This study demonstrated that soil and vegetation had changed in restored freshwater wetlands since agricultural abandonment. After 20 years of passive restoration, the typical plant communities of wetlands were close to those in natural wetlands. SOC and TN in the 10–30 cm soil layers required 8 and 13 years of restoration to reach the levels of natural wetlands, whereas those in the surface soil layer (0–10 cm) required 20 and 16 years of restoration, respectively. Although the asynchrony existed in this study, plant and soil interactions along restoration age were observed. The accumulations of carbon and nitrogen in restored wetlands depended on soil physical properties and vegetation properties including biomass and diversity. Therefore, passive restoration after agricultural abandonment can be used as an effective measure for degraded freshwater wetlands on the Sanjiang Plain. A further study is needed that focuses on investigating how soil nutrient accumulations interact with plant functional traits to reveal the restoration mechanisms in wetlands.

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