Research Article

A natural tropical freshwater wetland is a better climate change mitigation option through soil organic carbon storage compared to a rice paddy wetland

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Received: 7 January 2020 / Accepted: 11 April 2020 / Published online: 23 April 2020

Abstract
The high productivity together with hypoxic conditions in sediments enables wetlands to accumulate large amounts of soil organic carbon (SOC). However, natural tropical freshwater wetlands are increasingly being converted into other land uses, mainly rice cultivation. In this study, we investigated the impact of conversion of a natural tropical freshwater wetland into a rice paddy wetland on SOC, by determining SOC content, density and storage potential in the natural section (under different vegetation communities dominated by *Cyperus papyrus* [Papyrus], *Typha latifolia* [Typha] and *Phragmites mauritianus* [Phragmites]) and in the converted section (under rice cultivation). The SOC contents (g kg^{-1}) and densities (kg m^{-2}) of the 3 vegetation communities (Papyrus; 123.7 ± 2.6 [SE] and 7.22 ± 0.11, Typha; 85.3 ± 1.1 and 6.71 ± 0.12, and Phragmites; 78.2 ± 3.4 and 6.20 ± 0.06, respectively) of the natural section of the wetland were significantly higher ($p < 0.05$) than those (39.7 ± 0.7 and 3.90 ± 0.06, respectively) of the converted section. Similarly, for the entire sampled soil depth (0–50 cm), SOC storage potentials (Mg ha^{-1}) of Papyrus (361.18 ± 5.53), Typha (335.31 ± 6.18) and Phragmites (310.17 ± 3.16) significantly exceeded ($p < 0.05$) that obtained in the converted section by nearly 46%, 42% and 38%, respectively. Soil physico-chemical characteristics: bulk density, salinity, pH and temperature, showed comparably significant correlations ($p < 0.05$) with SOC in both the natural and converted sections of the wetland. We strongly believe that exploration of alternative options for increasing rice production outside wetlands is paramount if natural tropical freshwater wetlands are to remain important ecosystems in climate change mitigation.

Keywords Papyrus · Phragmites · Typha · Uganda · Vegetation community · Wetland conversion

1 Introduction

Due to global warming and the subsequent climate change, it is increasingly becoming of interest and vital to the scientific community to understand and quantify carbon pools and fluxes in terrestrial ecosystems such as wetlands [1–3]. On the other hand, minimizing carbon emission to the atmosphere and increasing the capture and long-term storage of atmospheric carbon dioxide have been considered a win–win strategy for climate change mitigation [1, 3].

Soil organic carbon (SOC) storage presents an inexpensive yet effective option for mitigating climate change [4]. Globally, soils store the largest terrestrial C pool, about thrice and twice higher than what is stored in vegetation and the atmosphere, respectively [5]. Thus, a small

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SN Applied Sciences (2020) 2:951 | https://doi.org/10.1007/s42452-020-2746-8

change in SOC pool may have a significant impact on climate change. The high productivity of natural wetlands together with the hypoxic/anoxic conditions enables them to accumulate large amounts of organic carbon in their soils [3, 6–8]. For example, wetlands are estimated to contain 20–30% of the earth's soil carbon pool, despite covering only 5–8% of the earth's surface [6]. More importantly, the high and relatively invariable temperatures in tropical regions induce high production rates of wetlands, which increases organic matter input in soil. Natural tropical wetlands are therefore widely recognized as promising C sinks, given that they cover approximately 30% of the world's wetlands area [9]. However, the most recent global wetland inventories [10–12] highlight an increasing rate of conversion of natural tropical freshwater wetlands into other wetland types, mainly rice paddy wetlands. In Uganda for instance, [13] has estimated current annual wetland loss at 846 km^2 (about 2% of total wetland cover), and rice cultivation is identified as one of the leading causes of wetland conversion in the country [14]. Such a trend raises concerns on the future role of natural tropical freshwater wetlands in global climate change mitigation.

Carbon storage in wetland soil is a function of both primary productivity and organic matter decomposition. Land use change is recognized as an important factor that influences SOC quantity and quality in wetland soil [15], because it alters vegetation and water table characteristics [6]. The top soil layer in wetlands is generally composed of the living root zone, and is most geomorphically unstable [6]. This implies that SOC stock of the top soil in wetlands is more susceptible to land use change compared to deep-soil SOC. With specific reference to agricultural land use change, SOC stocks of natural ecosystems are known to decrease following conversion into plantation or cropland [15–17]. However, SOC stocks in rice paddy wetlands have been shown to be highly variable depending on management practices [18–22]. For example, application of nitrogen fertilizer, manure, conservation tillage, and crop residues significantly increased SOC stocks of a rice paddy wetland from 107 to 121 kg ha^{-1} yr^{-1}, 159 to 326 kg ha^{-1} yr^{-1}, 78 to 128 kg ha^{-1} yr^{-1}, and 489 to 1005 kg ha^{-1} yr^{-1}, respectively [20]. Rice paddy fields transitioned from net carbon sinks at a nitrogen fertilizer application rates of between 0 and 300 kg ha^{-1} to net carbon sources at an application rate of 375 kg ha^{-1}. Modification of water depth affected carbon sequestration in a rice paddy wetland, while maintaining the water table depth at − 5 cm below the soil surface significantly increased carbon sequestration [22]. A 4-years experiment by [19] showed that rice paddy fields under no tillage had SOC of 129.32 Mg ha^{-1}, significantly higher than those of fields under conventional tillage (121.12 Mg ha^{-1}) and rotary tillage (125.09 Mg ha^{-1}). Variation of carbon sequestration in rice paddy soils based on changes in rice plant variety was reported by [18]. With these results, consequently, SOC stocks are expected to vary from one rice paddy wetland to another, depending on the management practices employed.

Most of the existing literature on rice paddy wetlands in Africa and Uganda in particular has given much attention to rice yields rather than carbon storage [23–26]. This limits an understanding of SOC stocks of rice paddy wetlands in this region. Therefore, to improve the accuracy of global SOC accounting and climate change models, it is a prerequisite to have a good understanding of SOC stocks in different ecosystems spread across the globe right from local scales. Further, in the face of climate change, comparative studies of SOC stocks in natural and rice paddy wetlands are a prerequisite for informed decision-making concerning wetland management in view of climate change mitigation as an ecosystem service. This is true, because some studies still indicate lack of consensus on the influence of rice cultivation on wetland SOC stocks [16, 20, 27, 28]. In this study, we investigated the impact of conversion of a natural tropical freshwater wetland into a rice paddy wetland on SOC, by comparing SOC content, density and storage potential in the natural section (under three naturally occurring dominant vegetation communities) and in the converted section, where natural vegetation was replaced by rice cultivation.

2 Materials and methods

2.1 Study area

The study was conducted on Naigombwa wetland, located in Iganga District, Southeastern Uganda. This wetland is part of the Lake Kyoga and River Nile basin wetland systems of Uganda (Fig. 1). The wetland can be divided into two sections, based on land use; natural and converted. The natural section can further be sub-divided into three different parts, in view of dominant wetland vegetation communities that form a permanent cover throughout the year: *Cyperus papyrus*, *Typha latifolia* and *Phragmites mauritianus*. These are also the common vegetation types in Ugandan wetlands. For simplicity in the proceeding text, *Cyperus papyrus*, *Typha latifolia* and *Phragmites mauritianus* are referred to as "Papyrus", "Typha", and "Phragmites", respectively.

The converted section occurs upstream of the natural section, where natural vegetation was replaced with rice cultivation. In the context of this study, the term "converted section" is therefore exclusively used to refer to the area under rice cultivation, a section also commonly known as rice paddy wetland. The rice is grown under

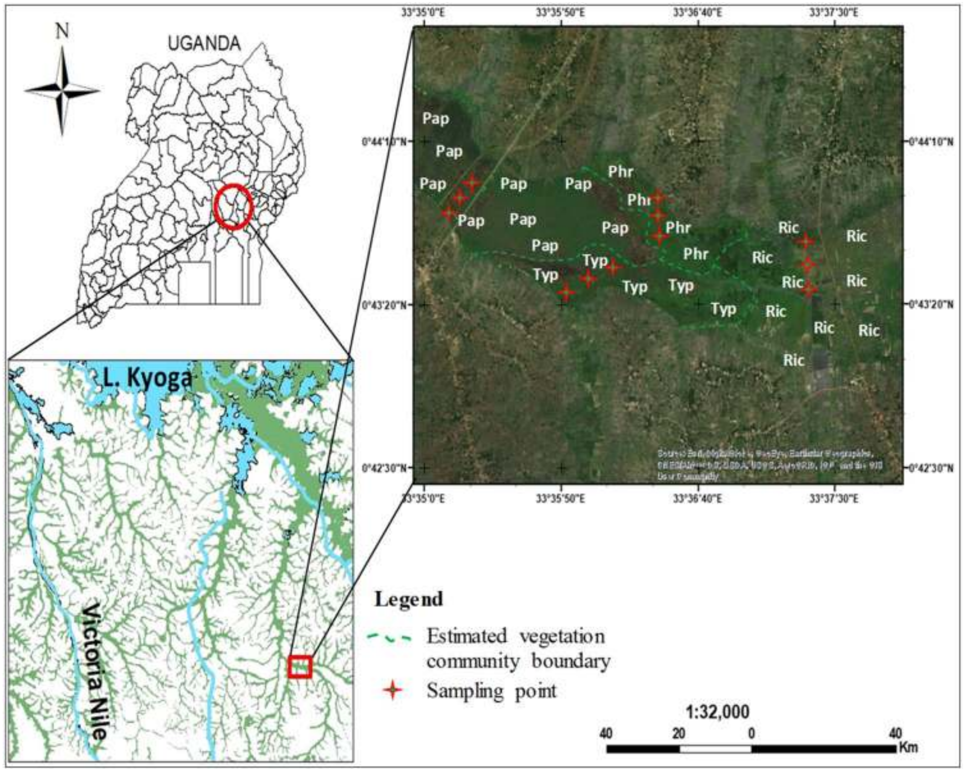


Fig. 1 Location of study area on the map of Uganda, and in the Lake Kyoga and River Nile basins. The specific sampled area was zoomed and geo-referenced from Google Earth. Pap = Papyrus, Typ = Typha, Phr = Phragmites, Ric = Rice

flood irrigation, using natural gravity flow of surface water from the catchment. Rice is planted either through broadcasting of rice grains, or through transplanting rice seedlings from nursery beds into the fields. There is no specified planting density of rice plants, while planting seasons are limited to two in a year. Basing on the information provided by rice farmers, the ages of sampled rice fields were in the range of 1–5 years. The farmers clarified that they had not previously witnessed human activities in the wetland areas where they were cultivating rice. This implies that the given ages of the rice fields represented the period since conversion of the wetland area from its natural state.

The water level in Naigombwa wetland varies during different seasons of the year [29]. Edges of the natural section of the wetland tend to experience intermittent flooding and drying cycles during wet and dry seasons, respectively. However, areas away from the edges are mainly flooded throughout the year, though the water level depth fluctuates between wet and dry seasons. In the converted section, intermittent flooding and drying regimes are also experienced during wet and dry seasons, respectively. However, unlike the natural section of the wetland, both the level and duration of flooding during the wet season in this section are manually regulated depending on the need, and both are generally lower than in the natural section. Throughout the sampling period, water was above the soil surface in both sections of the wetland. Mean recorded water levels were as follows : 34.6 ± 7.9 (SE) cm, 11.3 ± 2.6 cm and 5.3 ± 1.5 cm in the Papyrus, Typha and Phragmites vegetation communities of the natural section, respectively, and 2.3 ± 0.5 cm in the converted section.

Existing historical data (1961–1990) of weather stations in the Lake Kyoga basin show average annual temperature of 21 °C and annual rainfall of 1 300 mm, occurring on a bimodal pattern, from March to May and September to November [29]. In recent years however, unpredictable rainfall patterns in terms of period of onset and secession, frequency and intensity are being experienced [30].

2.2 Collection and analysis of soil samples

Soil sampling was done in the three vegetation communities of the natural section and in the converted section (rice fields) of the wetland. Three 1 m^2 sampling plots were randomly selected along transects established in each vegetation community of the natural section, and in the converted section (see Fig. 1 for locations of sampling points). The lengths of the transects varied depending on the spatial extent of the vegetation community and rice field, but ranged from 50 to 100 m. In each sampling plot, four cores (50 cm deep by 5.0 cm wide) were taken using a Russian peat borer [31]. The thin, sharp-walled edges of this borer provide for coring without compaction, distortion and disturbance. Each core was sectioned with a blade at 10 cm increments. One of the four cores at each sampling plot was used for bulk density measurement. The core depth was restricted to 50 cm following preliminary coring trials that established this depth as the possible maximum, beyond which there was compacted clay that made it difficult to drive the peat borer further.

Composite samples (three replicate composites at each sampling plot) were obtained by mixing three samples of the same depth in each sampling plot. Differences in SOC pools in the same sampling plot that might occur due to variations in decomposition were accounted for by spacing cores in a triangular pattern, 40 cm between each other as described by [32, 33]. With triplicates, 45 composite samples were obtained for each depth increment in each vegetation community. Composite samples were placed in labelled ziploc polyethylene bags and transported to the Soil Science Laboratory, College of Agricultural and Environmental Sciences, Makerere University, Kampala, Uganda for analysis.

Prior to analysis, composite soil samples were remixed to increase homogeneity, and visible plant residues were manually removed. The samples were air dried at room temperature for 21 days, ground and sieved through a 2 mm nylon sieve. Dry soil samples were used for determination of soil organic matter (SOM) content and soil physico-chemical characteristics (pH, salinity and nitrogen [N]). To determine SOM, 2 g of each soil sample (in triplicate) was placed in pre-weighed crucibles and pretreated with 10 M HCl until zero bubbling was achieved to prevent possibilities of carbonate interference [31, 34]. The samples were then dried in an oven (CARBOLITE CWF 13/5) at 105 °C until constant weight before being ignited at 450 °C for 4 h [31, 32]. Soil organic matter percentage (SOM%) of each sample was calculated following weight loss on ignition (LOI) as per Eq. (1), from where SOC percentage (SOC%) was obtained as a portion of SOM%, using Van Bemmelen's index of 0.58 [31]:

where SOCi % is the SOC % of layer i, Dbi is the bulk density at layer i (g cm^{-3}) and hi is the depth of soil layer i (cm).

Soil pH and salinity were determined using a multi-parameter metre (CyberScan PC 300), after equilibration of soil with deionized water (soil: water, 1:5) [35, 36]. Soil N content was determined using Kjeldahl digestion procedure [35, 36]. Bulk density (Db) was determined by drying a known volume of soil sample (determined from the dimensions of the core) at 105 °C until it reached a constant weight, cooled to room temperature in a desiccator, and weighed again. Bulk density was then expressed as dry weight of soil per unit volume [35]. Because all sites were fully submerged, there was no need for measurement of soil moisture content.

2.3 In situ measurements, and collection and analysis of plant samples

Soil temperature was measured in-situ using a digital soil thermometer. Plants (Papyrus, Typha, Phragmites, and rice) were destructively harvested in 0.3 m^2 triplicated plots along each transect for determination of biomass density (above and below ground), N and organic C contents. For above ground biomass, all plants in each sampling plot were harvested by cutting at the base and weighed to establish the total fresh weight. Plant parts below the soil surface (below ground biomass) were carefully removed to prevent root breakage, washed to remove all the soil and other attached material and weighed to establish the total fresh weight. Except samples of rice plants, which were all carried (because of their low biomass density), portions of Papyrus, Typha and Phragmites plant samples were carried to the laboratory for analysis of plant biomass (as dry weight). For N content, portions of plant parts (roots, stems and leaves) were mixed to make representative samples. In total, 45 composite plant samples were obtained

$$\text{SOM}\ (\%) = \frac{\text{Constant weight at } 105\,^\circ\text{C} - \text{Constant weight at } 450\,^\circ\text{C}}{\text{Constant weight at } 105\,^\circ\text{C}} * 100 \tag{1}$$

SOC content (g kg^{-1}) and SOC density (kg m^{-2}) for each soil layer, and SOC storage potential (Mg ha^{-1}) along the entire sampled 50 cm soil depth were, respectively, determined as depicted in Eqs. (2) [32], (3) [31] and (4) [35]:

$$\text{SOC content} = 10 * \text{SOCi}\% \tag{2}$$

$$\text{SOC density} = \text{SOCi}\% * \text{Dbi} * \text{hi} \tag{3}$$

$$\text{SOC storage potential} = \sum_{i=1}^{n} \text{SOCi}\ \% * \text{Dbi} * \text{hi} \tag{4}$$

from each vegetation community in the natural section, and in the converted section (rice fields) wetland.

Plant biomass (dry) was obtained from dry-to-wet weight ratio, after drying plant samples at 105 °C to a constant weight. Plant biomass density was expressed as the dry weight of plants per unit area. To determine plant N content, plant samples were oven dried at 65 °C until constant weight and ground [37], after which N content was determined using Kjeldahl digestion procedure [35, 36]. Plant organic C content was determined from the weight loss on ignition (LOI) procedure, as described for determination of SOC.

2.4 Data analysis

Statistical analysis was carried out in Microsoft Excel (2016) and R programming software (version 3.2.2). Data were first tested for normal distribution and homogeneity of variance, and were found to satisfy these conditions. As a result, one-way ANOVA and Tukey HSD post hoc test were used to determine the vertical and spatial variation of SOC content and density, and storage potential between natural and converted sections of the wetland, at a significance level of 95% ($p < 0.05$) [31, 34]. The relationships between soil physico-chemical and plant characteristics and SOC were determined using Spearman rank correlation, at a significance level of 95% ($p < 0.05$).

3 Results

3.1 Soil physico-chemical and plant characteristics

Most soil physico-chemical parameters varied with soil depth in both sections of the wetland. Temperature, salinity and N content generally decreased with increasing soil depth. On the other hand, pH and bulk density generally increased with increasing soil depth (Table 1).

Soil temperature was highest in the converted section, which also showed the greatest drop in soil temperature from the top (0–10 cm) to the bottom (40–50 cm) soil layer of 0.7 °C, compared to 0.5 °C, 0.4 °C and 0.3 °C

Table 1 Soil physico-chemical characteristics at different depths in the different sections of the wetland. Values are mean ± SE ($n = 45$)

Parameter	Wetland section	Soil depth (cm)					
		0–10	10–20	20–30	30–40	40–50	Mean (0–50)
Temperature (°C)	Natural						
	Papyrus	26.6 ± 0.0	26.5 ± 0.1	26.4 ± 0.1	26.3 ± 0.1	26.2 ± 0.0	26.4 ± 0.1^a
	Typha	26.9 ± 0.1	26.7 ± 0.1	26.5 ± 0.2	26.4 ± 0.2	26.4 ± 0.2	26.6 ± 0.1^a
	Phragmites	26.6 ± 0.1	26.4 ± 0.1	26.4 ± 0.1	26.4 ± 0.1	26.3 ± 0.0	26.4 ± 0.1^a
	Converted (rice fields)	27.8 ± 0.1	27.7 ± 0.1	27.6 ± 0.1	27.5 ± 0.1	27.1 ± 0.1	27.5 ± 0.1^a
pH	Natural						
	Papyrus	5.29 ± 0.01	5.74 ± 0.01	5.94 ± 0.02	6.12 ± 0.03	6.34 ± 0.01	5.88 ± 0.02^a
	Typha	6.23 ± 0.01	6.26 ± 0.02	6.67 ± 0.02	7.00 ± 0.01	7.07 ± 0.06	6.64 ± 0.02^a
	Phragmites	6.06 ± 0.01	6.34 ± 0.01	6.50 ± 0.04	6.80 ± 0.01	6.88 ± 0.01	6.52 ± 0.01^a
	Converted (rice fields)	7.47 ± 0.03	7.34 ± 0.02	8.24 ± 0.04	8.60 ± 0.10	8.81 ± 0.02	8.09 ± 0.04^b
	Natural						
Salinity (mS m^{-1})	Papyrus	406.86 ± 7.45	169.68 ± 2.03	87.62 ± 1.19	55.79 ± 5.29	66.51 ± 2.91	157.29 ± 3.77^a
	Typha	129.22 ± 2.40	122.64 ± 0.95	120.66 ± 2.37	88.81 ± 7.25	61.74 ± 0.44	104.61 ± 2.68^a
	Phragmites	118.59 ± 2.48	64.09 ± 0.33	46.30 ± 1.08	34.25 ± 0.28	33.17 ± 0.15	59.27 ± 0.86^b
	Converted (rice fields)	56.25 ± 0.25	49.45 ± 1.59	48.71 ± 0.70	43.38 ± 0.17	41.00 ± 2.05	47.76 ± 0.95^b
Bulk density (g cm^{-3})	Natural						
	Papyrus	0.46 ± 0.01	0.58 ± 0.02	0.65 ± 0.03	0.79 ± 0.02	0.81 ± 0.03	0.66 ± 0.02^a
	Typha	0.67 ± 0.01	0.68 ± 0.01	0.82 ± 0.01	0.84 ± 0.01	0.92 ± 0.01	0.79 ± 0.01^a
	Phragmites	0.38 ± 0.01	0.58 ± 0.06	0.92 ± 0.04	1.00 ± 0.01	1.10 ± 0.12	0.76 ± 0.05^a
	Converted (rice fields)	0.75 ± 0.09	0.83 ± 0.06	1.03 ± 0.05	1.15 ± 0.04	1.16 ± 0.02	0.98 ± 0.05^a
N (%)	Natural						
	Papyrus	0.83 ± 0.03	0.44 ± 0.01	0.31 ± 0.01	0.29 ± 0.01	0.21 ± 0.01	0.42 ± 0.01^a
	Typha	0.43 ± 0.01	0.34 ± 0.01	0.32 ± 0.01	0.26 ± 0.01	0.26 ± 0.03	0.32 ± 0.01^a
	Phragmites	0.50 ± 0.01	0.47 ± 0.01	0.32 ± 0.01	0.20 ± 0.01	0.20 ± 0.01	0.34 ± 0.01^a
	Converted (rice fields)	0.29 ± 0.01	0.26 ± 0.02	0.15 ± 0.01	0.13 ± 0.01	0.13 ± 0.01	0.20 ± 0.01^a
C:N	Natural						
	Papyrus	29.9:1 ± 4.9:1	34.4:1 ± 5.4:1	35.0:1 ± 6.6:1	28.5:1 ± 6.5:1	32.3:1 ± 5.0:1	32.0:1 ± 4.1:1^a
	Typha	29.3:1 ± 5.5:1	28.8:1 ± 4.6:1	24.0:1 ± 2.7:1	28.8:1 ± 4.1:1	24.0:1 ± 2.4:1	27.0:1 ± 5.1:1^a
	Phragmites	41.2:1 ± 3.7:1	22.7:1 ± 4.2:1	20.3:1 ± 2.6:1	28.1:1 ± 5.3:1	24.6:1 ± 4.1:1	27.4:1 ± 3.2:1^a
	Converted (rice fields)	21.3:1 ± 4.8:1	20.8:1 ± 3.3:1	26.7:1 ± 3.2:1	21.0:1 ± 2.0:1	20.1:1 ± 7.4:1	22.0:1 ± 3.5:1^a

C Carbon, *N* Nitrogen

Superscript letters indicate statistical difference at $p < 0.05$

in Typha, Papyrus and Phragmites vegetation communities, respectively, of the natural section of the wetland.

The pH values in all the three vegetation communities of the natural section of the wetland were generally acidic, contrasting from those in the converted section that were in the alkaline region. On average, pH in the converted section was 2.21, 1.57 and 1.45 units higher than in the Papyrus, Phragmites and Typha vegetation communities, respectively.

Salinity showed a great variation with soil depth, and between natural and converted sections of the wetland, and it was on average highest in the natural section. For example, salinities of the top (0–10 cm) soil layer in the Papyrus, Phragmites and Typha vegetation communities were over 83%, 72% and 52% higher than those at the bottom (40–50 cm) layer, respectively, compared to only 27% in the converted section of the wetland.

Bulk density was highest in the converted section of the wetland, though variations between the two wetland sections were small. Average bulk density of the converted section of the wetland exceeded the natural section by 0.33 g cm^{-3}, 0.19 g cm^{-3} and 0.23 g cm^{-3} (in view of Papyrus, Typha and Phragmites vegetation communities, respectively). Nitrogen (N) content also showed minimal variations with soil depth and between natural and converted sections of the wetland. Average values of N content in the Papyrus, Typha and Phragmites vegetation communities exceeded that in the converted section by only 0.22%, 0.12% and 0.14%, respectively. Soil C:N ratio did not show any clear trend with soil depth, but was higher in the natural section of the wetland.

Plant characteristics also varied amongst the wetland sections (Table 2). Plant biomass density was highest in the natural section of the wetland. Above ground and below ground biomass densities of the Papyrus vegetation community were above 12 and 17 folds, respectively, higher than in the converted section, followed by the Typha vegetation community, whose both biomass densities were, respectively, over 10 and ninefolds greater than in the converted section. Above and below ground biomass densities in the Phragmites vegetation community were also considerably higher than in the converted section, with respective differences of over seven and eight folds. Both plant C and N contents were highest in the converted section of the wetland, differing from the lowest observed values in the natural section (Typha vegetation community) by 8.4% and 0.8% in that order. However, C:N ratio followed the order: natural section (Typha vegetation community > Papyrus vegetation community > Phragmites vegetation community) > converted section.

3.2 Soil organic carbon in the natural and converted sections of the wetland

Both SOC content and density presented notable variations in vertical and spatial distribution. They both generally decreased with increase in soil depth in both sections of the wetland (Figs. 2 and 3, respectively). Changes in SOC contents and densities were observed in all soil layers, in order of decreasing magnitude: 0–10 cm > 10–20 cm > 20–30 cm > 30–40 cm > 40–50 cm. However, the decrease was most pronounced in the natural section than the converted section of the wetland. For instance, SOC content decreased (from the top [0–10 cm] to the bottom [40–50 cm] soil layer) by over 66% in the natural section (taken as an average of Papyrus, Typha and Phragmites vegetation communities) compared to about 57% in the converted section. Similarly, SOC densities of these two soil layers differed by over 25% in the natural section compared to only about 15% in the converted section. However, in both sections of the wetland, the top 20 cm accounted for more than half of the total SOC content, while the top 30 cm had more than 64% of the total SOC density.

All the three vegetation communities (Papyrus, Typha and Phragmites) of the natural section of the wetland had both SOC contents and densities significantly higher ($p < 0.05$) than in the converted section at all soil layers. However,

Table 2 Plant characteristics in the different wetland sections. Values are Mean ± SE ($n = 45$)

Wetland section	Plant characteristics				
	Biomass density (kg m^{-2})		C (%)	N (%)	C:N
	Above ground	Below ground			
Natural					
Papyrus	8.72 ± 0.84^a	10.77 ± 0.51^a	29.16 ± 0.80^a	0.67 ± 0.07^a	$43.5{:}1 \pm 9.8{:}1^a$
Typha	7.55 ± 1.13^{ab}	7.36 ± 0.17^b	23.86 ± 1.65^b	0.48 ± 0.01^a	$49.9{:}1 \pm 10.4{:}1^a$
Phragmites	5.51 ± 0.42^b	6.81 ± 0.13^b	25.10 ± 0.13^b	0.62 ± 0.03^a	$40.5{:}1 \pm 9.2{:}1^a$
Converted (rice fields)	0.72 ± 0.06^c	0.79 ± 0.03^c	32.24 ± 0.67^a	1.24 ± 0.08^b	$25.9{:}1 \pm 18.11^a$

C Carbon, *N* Nitrogen

Superscript letters indicate statistical difference at $p < 0.05$

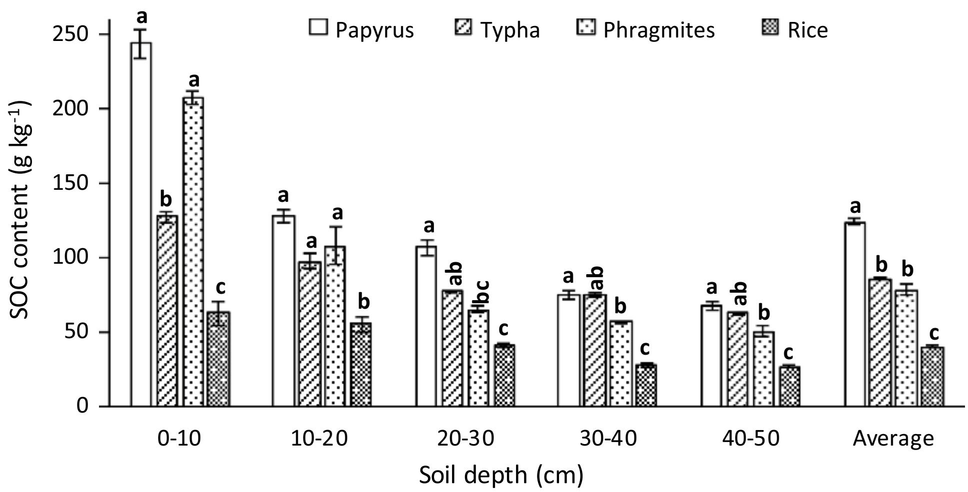


Fig. 2 Comparison of SOC contents at different depths in the natural (Papyrus, Typha and Phragmites) and converted (rice) sections of the wetland. Error bars are standard errors (SE) of the mean. Grouped bars (for each soil depth category) with different letters are significantly different (Tukey HSD, $n = 45$, $p < 0.05$)

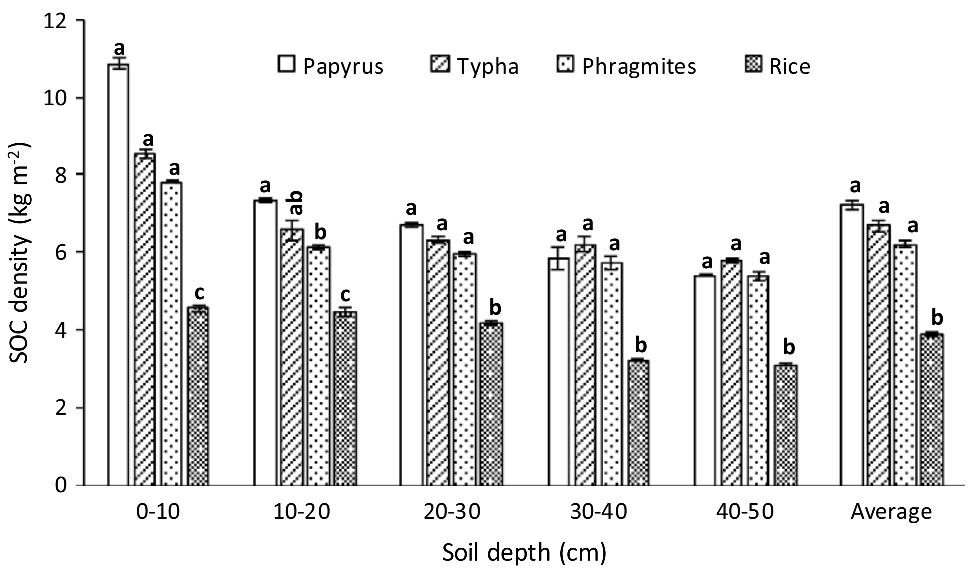


Fig. 3 Comparison of SOC densities at different depths in the natural (Papyrus, Typha and Phragmites) and converted (rice) sections of the wetland. Error bars are standard errors (SE) of the mean. Grouped bars (for each soil depth category) with different letters are significantly different (Tukey HSD, $n = 45$, $p < 0.05$)

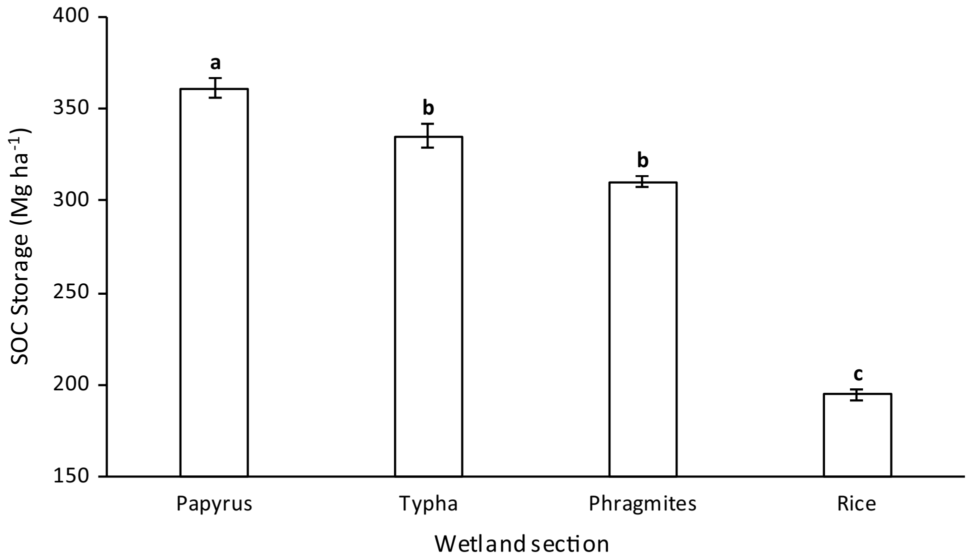
the magnitude of variation was most pronounced at the top (0–10 cm) soil layer, and decreased with increase in soil depth. On average, SOC contents and densities of the all the three vegetation communities of the natural section of the wetland were higher than those recorded in the converted section with significant amounts ($p < 0.05$). For example, average SOC contents of Papyrus (123.7 ± 2.6 [SE] g kg^{-1}), Typha (85.3 ± 1.1 g kg^{-1}) and Phragmites (78.2 ± 3.4 g kg^{-1}) vegetation communities exceeded that of the converted section (39.7 ± 0.7 g kg^{-1}) by over threefold, twofold and close to twofold, respectively. Similarly, average SOC density in Papyrus (7.22 ± 0.11 [SE] kg m^{-2}), Typha (6.71 ± 0.12 kg m^{-2}) and Phragmites (6.20 ± 0.06 kg m^{-2}) were higher than that (3.90 ± 0.06 kg m^{-2}) of the converted section. Since SOC density was obtained as a function of SOC content and bulk density (which was highest in the converted section; Table 1), the lower SOC density observed in the converted section indicates that SOC density was mainly dictated by SOC content rather than bulk density.

In consideration of SOC storage potential for the entire sampled soil depth (0–50 cm), all the three vegetation communities of the natural section of the wetland had SOC pools higher than the converted section, with significant magnitudes ($p < 0.05$, Fig. 4). The SOC storage potentials of Papyrus (361.18 ± 5.53 [SE] Mg ha^{-1}), Typha (335.31 ± 6.18 Mg ha^{-1}) and Phragmites (310.17 ± 3.16 Mg ha^{-1}) vegetation communities were nearly 46%, 42% and 38%, respectively, greater than that (195.10 ± 2.82 Mg ha^{-1}) of the converted section.

3.3 Relationship between soil physico-chemical and plant characteristics and SOC

The relationship between soil physico-chemical and plant characteristics and SOC were comparable (both in terms of

Fig. 4 SOC storage potential of the natural (Papyrus, Typha and Phragmites) and converted (rice) sections of the wetland. Error bars are standard errors (SE) of the mean. Bars with different letters are significantly different (Tukey HSD, $n = 27$, $p < 0.05$)



magnitude and direction) in both sections of the wetland, as reflected by the Spearman rank correlation coefficients (Table 3). With respect to the significance of correlations, plant biomass density, and soil physico-chemical characteristics: bulk density, salinity, pH and temperature presented significant correlations ($p < 0.05$) with SOC in that order of decreasing magnitude in both sections of the wetland. On the other hand, soil C:N ratio insignificantly correlated ($p > 0.05$) with SOC. In view of direction of the correlations, plant biomass density, soil salinity, and temperature and C:N ratio were positively correlated with SOC, unlike pH and bulk density that exhibited negative correlations with SOC.

4 Discussion

4.1 Soil organic carbon in the natural and converted sections of the wetland

In the present study, SOC content and density were decreasing with soil depth in both the natural and converted sections of the wetland (Figs. 2 and 3). Other studies have also reported similar trends in natural tropical freshwater wetland soils [31, 32, 35–38] and in rice paddy wetland soils [5, 15]. This occurrence is associated with the continuous input of freshly dead plant biomass on the top soil layers [3, 35]. Cases of harvesting standing plant biomass in the natural section of the wetland were rarely observed, and of minor significance. Even in the converted section, rice plants were being left in the fields after harvesting. This implies (for both the natural and converted sections) that plant biomass is continuously added to the

Table 3 Spearman rank correlations between SOC and soil salinity, pH, temperature, bulk density, C:N ratio, and plant biomass density in natural and (converted) sections of the wetland ($n = 45$)

	SOC	pH	Sal	Temp	Db	C:N	Plant BmD
SOC	1.00 (1.00)						
pH	−0.79* (−0.81*)	1.00 (1.00)					
Sal	0.83* (0.85*)	−0.74* (−0.86*)	1.00 (1.00)				
Temp	0.68* (0.70*)	−0.27 (−0.34)	0.41 (0.71*)	1.00 (1.00)			
Db	−0.89* (−0.88*)	0.79* (0.75*)	−0.64* (−0.68*)	−0.46 (−0.32)	1.00 (1.00)		
C:N	0.46 (0.48)	0.55 (0.51)	−0.18 (−0.24)	0.13 (0.20)	0.47 (0.42)	1.00 (1.00)	
Plant BmD	0.98* (0.95*)	−0.43 (−0.40)	0.48 (0.47)	−0.73* (−0.69*)	−0.34 (−0.46)	−0.05 (−0.22)	1.00 (1.00)

Sal salinity, *Temp* temperature, *Db* bulk density, *BmD* biomass density, *C* carbon, *N* nitrogen

*Significant at $p < 0.05$

top soil, hence increasing the SOM and the subsequent SOC compared to deep soil layers. However, the converted section of the wetland had a less pronounced variation of SOC content and density between top and bottom soil layers compared to the natural one. This could be attributed to tillage-induced soil mixing along the soil profile [19].

In view of magnitude of variation of SOC content, density and storage potential, all the three vegetation communities of the natural section of the wetland had values significantly greater than what was recorded in the converted section. Our reasoning for this observation relates to differences of three aspects: 1) primary productivity [36, 39], 2) organic matter recalcitrance [34, 40], and 3) flooding regimes [8, 32], between the natural and converted sections of the wetland. Plant biomass is the main source of SOM and the subsequent SOC in wetlands [3, 15]. Therefore, a high primary productivity is likely to translate into high SOC. Natural tropical freshwater wetlands have already been described by some of the highest rates of primary productivity of any ecosystem [1, 39, 41]. Unlike the converted section of the wetland (rice fields) where plant biomass productivity is limited to the growing seasons, productivity of plants in the natural section is continuous year-round, ensuring uninterrupted input of SOM into the soil. Further, the specific macrophytes in the natural section of the wetland under this study have been reported to be amongst the most productive wetland plants. In Africa for example, [39] have found net primary productivity of Papyrus wetlands ranging between 2.51 and 3.09 kg m^{-2} yr^{-1}, and suggested that they represent one of the highest productivity rates recorded in any natural ecosystem. Net primary productivities of Papyrus and Typha vegetation communities in littoral wetlands of Lake Ziway, Ethiopia were 2.39 kg m^{-2} yr^{-1} and 2.20 kg m^{-2} yr^{-1}, respectively, higher than any other wetland macrophyte in the area [42]. The net primary productivity of Phragmites in tropical wetlands has also been reported, ranging from 0.88 to 2.2 kg m^{-2} yr^{-1} [43, 44]. Though data on net primary productivity of rice plants is not readily available due to great variations in soil and cropping management practices [45], an estimate by [46] showed that it's over six times less than that of macrophytes in natural wetlands. We obtained biomass densities in all sections of the natural section of the wetland in an order of magnitude greater than in the rice fields, supporting the high productivity of natural wetlands. Further, to enhance SOC accumulation in rice paddy soils, studies [5, 26, 27, 47] have suggested continuous cropping, with a view of increasing plant biomass production and the consequent organic matter input into the soil.

Organic matter recalcitrance is one of the most critical aspects of SOC in wetland soil. Studies by [34] and [40] attributed inequalities in SOC in wetlands under varying plant communities to differences in the degree of recalcitrance of organic matter from plant biomass input. Plant biomass rich in lignin is recalcitrant, making the resultant organic matter resistant to decomposition [32]. Nevertheless, though we did not investigate lignin contents of the respective plant biomass in our study, we think that organic matter from rice plant biomass is less recalcitrant (more labile), making it prone to rapid decomposition. Indeed, our argument is supported by [18], who established a lower lignin content (5–15%) of rice plant biomass, compared to 24% for Typha [48], 22–23% for Phragmites [49] and 12–34% for Papyrus [50]. Additionally, [5] observed that the biggest fraction of SOC pool in rice paddy soils exists as labile organic carbon.

In consideration of flooding regimes, the role of water table height in regulation of SOC has been widely documented [3, 6–8]. These studies show that organic matter decomposition increases with a decrease in water table height. This is an indication that SOC declines with a corresponding decline in water table height. In the natural section of this wetland, the soil is mainly permanently flooded throughout the year [30], though flooding and drying cycles are experienced close to the wetland edges. In the converted section (rice fields), however, flooding occurs only during the wet season, where the flooding level and duration is even regulated, and lower than in the natural section. The presence of drainage channels in this section of the wetland enhances water table drawdown, facilitating rapid drying up of rice fields during the dry season and hence promoting SOM decomposition and a consequent reduction in SOC storage.

Findings of SOC in the different sections of the wetland in this study are comparable to results of other studies. The content and density of SOC in a natural wetland in China were significantly higher than in a rice paddy wetland, 15 years after conversion to rice cultivation [15]. At different soil depths, SOC contents in the rice paddy wetland were 75–83% lower than those in the natural wetland. Total SOC density (15.98 kg m^{-2}) in the natural wetland was over 20% higher than that (12.74 kg m^{-2}) recorded in the rice paddy wetland. A similar study by [51] reported results both in agreement and contrast to ours. In terms of spatial variation of SOC between natural and rice paddy wetlands, the authors obtained SOC densities of natural wetlands at the top 60 cm and 100 cm as 23.50 kg m^{-2} and 29.59 kg m^{-2}, respectively, about 34% and 33% higher than those of rice paddy wetlands. These values translated into SOC storage potentials of 235.0 Mg ha^{-1} and 295.9 Mg ha^{-1} at the respective soil depths, compared to 155.3 and 19 7.9 Mg ha^{-1}, respectively, in the rice paddy wetlands. However, considering vertical distribution of SOC pools, our results contradict those of [51] who pointed out that

SOC densities in both natural and rice paddy wetlands increased with depth. Nonetheless, the study was carried out in a temperate environment, where SOC pools have already been reported to increase with increase in soil depth [7, 32, 33, 35]. On a global perspective, [2] reported average SOC density in freshwater marsh wetlands (same as our study wetland) as 38 kg m^{-2}, more than threefold that (12.1 kg m^{-2}) for rice paddy wetlands for the top 1 m soil depth.

Besides, it has been previously reported that a significant impact of agricultural land use change on soil carbon stock can only be noticed over a longer time (possibly on a decadal timescale) due to the inherently long-term stability of soil carbon [15, 27, 28, 52]. For example, [27] showed that 30–35% of the soil carbon stored in the top 7 cm was lost in the first 30 years after turning a forest into agricultural land, while no changes were observed below plough depth. However, our study showed significant changes in SOC stocks even at a short period, as our sampled rice fields only ranged 1–5 years old. The stability and duration of carbon in soil following agricultural land use change could therefore be variable depending on the characteristics of the original and new ecosystems [3].

With the already high concentration of greenhouse gases CO_2 and CH_4 in the atmosphere, achieving rapid climate change mitigation requires maximizing C storage [53]. The natural wetland section had nearly 46%, 42% and 38% (in view of Papyrus, Typha and Phragmites vegetation communities, respectively) higher SOC storage potential than the converted section. Therefore, assuming similar conditions in other natural wetlands of Uganda, conversion of the country's natural wetlands into rice paddy wetlands will approximately reduce the former's SOC storage potential by a range of 38–46%. This outcome implies a significant compromise on the ability of the country's natural wetlands to mitigate climate change. This argument especially resonates with the understanding that rice paddy wetlands also have a high emission potential of greenhouse gases to the atmosphere [5, 22]. In the same sense, consequently, whereas high demand for rice (as food) may be the major driver for conversion of freshwater tropical wetlands, other options for increasing rice production need to be explored. Some studies have reported a potential of increasing rice production using upland rice cropping systems [24, 54–56]. Otherwise, a cost–benefit analysis of climate change mitigation (in view of conventional carbon capture and storage technologies) versus rice production may be necessary to help inform decision on whether to conserve or convert natural tropical freshwater wetlands into rice paddy wetlands.

4.2 Relationship between soil physico-chemical and plant characteristics and SOC

It was observed that soil physico-chemical and plant characteristics had comparable relationships with SOC in both sections of the wetland. Soil bulk density, salinity, pH and temperature, and plant biomass density had significant impacts on SOC. Soil C:N ratio on the other hand showed an insignificant control on SOC. These results are not an exception as other studies have obtained related findings [8, 36, 57].

A significant negative correlation between SOC and bulk density was reported by [58], who explained that bulk density affects water infiltration, rooting depth, microbial activity and nutrient availability. These in turn, affect plant productivity and the consequent SOC turnover. Salinity has been shown to affect SOC pools by exerting a control on soil microbial respiration. Exposure of freshwater wetland soil to 3.5 g kg^{-1} saline (as sodium chloride) water increased SOC mineralization rate by 17% [57]. However, [59] observed that the influence of salinity on SOC pools is more important for tidal coastal freshwater wetlands that are usually subject to sea level rises. Temperature influences microbial metabolism and population dynamics, directly affecting SOM decomposition and SOC storage [8]. This was further emphasized by [60] who observed a doubling of SOM decomposition rates for every 10 °C temperature increase. In terms of pH, the activities of soil microbial communities involved in SOC turnover are at their optimum within a particular pH range. A study by [61] established that decomposition rates of plant biomass were negatively affected outside a pH range of 3.0–6.5. For rice paddy wetlands, [62] found SOC in rice fields with lower soil pH (4.66–5.10) greater than in fields with high soil pH (5.16–5.66), and attributed it to reduced microbial activity in the low soil pH rice fields. A strong positive correlation between plant biomass density and SOC stocks in natural [36, 37] and rice paddy [5] wetlands has been acknowledged.

An insignificant correlation between soil C:N ratio and SOC was observed by [36] in natural wetlands under different vegetation communities. This observation supports an earlier understanding by [63] that the influence of C:N ratio on SOC may be negligible in natural wetland soils with high SOC content. However, in rice paddy wetlands, other studies have established a significant correlation between C:N ratio and SOC [20, 58, 62]. Nonetheless, [21] have recently indicated that the correlation between C:N ratio and SOC pools is most expected to be significant in rice paddy wetlands where nitrogen fertilization is practiced. The explanation given is that soil nitrogen enhancement lowers the C:N ratio, stimulating microbial activity and corresponding SOM decomposition. This observation could help explain our findings, as fertilization of our study rice fields was not being practiced. Farmers depended on the natural fertility of soil, which minimizes manipulation of soil C:N ratio.

5 Conclusions

Both SOC content and density in the natural section (under Papyrus, Typha and Phragmites vegetation communities) and in the converted section (under rice cultivation) of a tropical freshwater wetland decrease with increasing soil depth. However, the decrease is more pronounced in the natural section than the converted section. In view of SOC storage potential for the sampled 0–50 cm soil depth, the natural section of the wetland stores nearly 46%, 42% and 38% more SOC (with respect to Papyrus, Typha and Phragmites vegetation communities) than the converted section. Therefore, assuming similar conditions in other natural wetlands of Uganda, conversion of the country's natural wetlands into rice paddy wetlands will approximately reduce the former's SOC storage potential of the top 50 cm soil layer by a range of 38–46%.

Plant biomass density is the most important factor controlling SOC pools in both the natural and converted sections of the wetland. In consideration of soil physicochemical characteristics, bulk density, salinity, pH and temperature exert comparably significant influences on SOC in both natural and converted sections of the wetland.

Basing on our findings, if the current trend of conversion of natural tropical freshwater wetlands into rice paddy wetlands is to continue, their role in climate change mitigation will be significantly reduced. As a result, we strongly believe that if natural tropical freshwater wetlands are to remain relevant in climate change mitigation, alternative options for increasing rice production outside wetlands need to be explored. Further, a cost–benefit analysis of climate change mitigation versus rice production can help make informed decisions on whether to conserve or convert natural tropical freshwater wetlands into rice paddy wetlands.

Acknowledgements This work was supported by African Center of Excellence for Water Management (ACEWM) (Grant No. ACEWM/GSR/9813/10), under the World Bank's African Centers of Excellence (ACE II) Project. We appreciate the local community members along Naigombwa wetland for the good hospitality and support during field sampling. Additional thanks go to the Department of Environmental Management, Makerere University for offering laboratory and sitting space. We finally, thank Ms. Aguttu Gorret for the extraordinary support during preparation and analysis of samples.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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