



Does Flood Pulsing Act as a Switch to Store or Release Sediment-Bound Carbon in Seasonal Floodplain Lakes? Case Study from the Colombian Orinoco-Llanos and the Brazilian Pantanal

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Received: 25 June 2013 / Accepted: 23 October 2013 / Published online: 6 December 2013
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Abstract Wetlands have been identified as key elements of global carbon budgets. Today, due to increasing anthropogenic carbon emissions, the carbon storage capacity of these ecosystems has become of global interest. The focus of this research was to determine the storage capacity and mechanisms of carbon sequestration of Neotropical seasonal shallow lakes (SSLs), assessing their flood pulse, biomass, geomorphology and sediment composition. We applied a standardized and extensive sampling to five SSLs from the Colombian Orinoco-Llanos and five from the Brazilian Pantanal, during both flooded and non-flooded seasons. We found that sediment organic carbon (SOC) storage capacity in SSLs is significantly driven by the number of flooded days (p -value = 0.0057) rather than by their biomass production. The Orinoco-Llanos and Pantanal lakes differ in morphology, and thus in their inundation patterns. SSLs of the Orinoco-Llanos are

more concave, having a significantly higher number of flooded days/year than SSLs from Pantanal. These hydrologic differences affect SOC storage, resulting in a significantly higher SOC storage in SSLs from Orinoco-Llanos than in Pantanal. A synopsis of data from both regions suggests the existence of a critical threshold between “non-flooded season losses” and “non-flooded season storage” of SOC in SSLs in a range of 225–275 flooded days/year.

Keywords Neotropical wetlands · Carbon storage · Geomorphology · Biomass · Sediment

Introduction

Today, as anthropogenic carbon emissions are increasing, the carbon storage capacity of aquatic and terrestrial ecosystems has become an important environmental issue. Wetlands have been identified as key carbon reservoirs, being net carbon sinks of about 830 Tg/year (Mitsch et al. 2012) in a relatively small area (2–8 % of the terrestrial land surface) (Mitsch and Gosselink 2007). Wetland types may have strong differences between them in their carbon pathways and stocks (Mittra et al. 2005; Adhikari et al. 2009). However, even within a given wetland type, there is a wide range of carbon stock estimations, making more detailed and compatible information about carbon deposits and sequestration processes necessary, particularly in tropical wetlands (Mittra et al. 2005; Mitsch et al. 2010).

Wetlands share characteristics with permanently terrestrial and aquatic ecosystems. However, they have unique features related to hydrology, biogeochemistry, productivity and food webs (Junk 1997; van der Valk 2006; Maltby 2009). The overarching parameter of wetlands, their hydrology, spans a

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wide range from permanent bogs to ephemeral ponds (Mitsch and Gosselink 2007). Seasonal wetlands are subject to a flooded-and-non-flooded cycle with variable dynamics of their hydrographs and different origins of floodwater. The Flood Pulse Concept (FPC) predicts that wetlands receiving riverine or lacustrine floodwater may have increased productivity in comparison to permanently aquatic or terrestrial ecosystems (Junk et al. 1989; Junk and Wantzen 2004; Wantzen et al. 2008b). Apart from the contribution of nutrients, the flood pulse has a rejuvenating effect on the floodplain system, as parts of the terrestrial production become consumed or removed during the aquatic phase and vice versa. Moreover, the annual and multi-annual variability of the hydrographic patterns is decisive for the development of different floral and faunal assemblages, as these patterns may match (windows of opportunity) or mismatch (windows of susceptibility) their preferred environmental settings, enabling the coexistence of different strategies for resource use, thus increasing biodiversity and productivity (Junk and Wantzen 2004).

The portion of the annual production that lastly remains stored in the system as living biomass or as soil organic carbon; depends on soil, hydrographic and vegetation properties, and the tight interplay between these factors (Zhang et al. 2002). In the floodplain forests of Central Amazonia, the largest part of the annual net production is stored in tree and soil biomass. It is estimated that the Brazilian Amazon stores more than 120 Pg (10^{15} g) of reduced carbon, 34 % of that being in soils and 66 % in aboveground vegetation (McClain 2001). North and south of this evergreen equatorial belt in South America, there are extensive seasonal biomes which contain large wetlands with globally outstanding biological and ecological status (Olson et al. 1998): these include the Colombian-Venezuelan Orinoco-Llanos to the North, and the Brazilian-Bolivian Pantanal to the South. The Pantanal, albeit smaller in area than the sum of the Central Amazonian wetlands, is considered the largest contingent wetland (160.000 km²) in the world (Junk et al. 2011; Junk and Nunes da Cunha 2012). On the other hand, the floodable Orinoco-Llanos have an area of 150.000 km² (Hamilton et al. 2004), being comparable with the Pantanal area. In spite of the large geographical distance between Orinoco-Llanos and Pantanal, the geological formation and climatological setting are very similar, resulting in similar floral assemblages in seasonal shallow lakes (SSLs) (Vega et al. unpublished manuscript). Both biomes have rarely been studied in relation to their carbon storage potential. In the Pantanal, studies by Nogueira et al. (2002) and Couto and Oliveira (2011) indicate a low carbon storage potential of its soils in general, and similar findings were reported for the Orinoco-Llanos in Venezuela by San-Jose et al. (1998, 2010) and Smith et al. (2000). To our knowledge there are no studies about carbon storage in the floodplain wetlands of the Orinoco-Llanos in Colombia.

Using a double-biome approach, we applied a standardized procedure and extensive sampling to SSLs from both Colombian Orinoco-Llanos and Brazilian Pantanal biomes, in order to compare the carbon storage in these large seasonal savannah floodplains.

In this study we explore the mechanisms of carbon sequestration, capacity to store carbon and carbon sink or source function of SSLs by analyzing their relationships with flood pulse pattern (number of flooded days/year), geomorphology (bathymetry) and seasonal biomass production, and sediment composition. Our working hypotheses were that (i) the length of the inundation period, (ii) the aboveground biomass stocks, or (iii) interactions between these parameters determine seasonal sediment organic carbon (SOC) storage capacity in SSLs.

In addition to our studies concerning carbon sequestration mechanisms and storage capacity, we aim to provide new insights into ecology and environmental services offered by these as-yet poorly studied SSLs, which are characteristic systems of the Orinoco-Llanos and the Pantanal. Thus, our study will contribute support to the development of wetlands classification systems, sustainable management concepts, and the definition of conservation goals in Colombia and Brazil.

Methods

Study Areas

The SSLs of our study develop at depressional sites of paleo-floodplains from the Orinoco-Llanos and the Pantanal (Irion et al. 2011). In these biomes the declivity of the landscape is very low (only of few centimeters per kilometer). SSLs undergo a pronounced annual hydrological variation, i.e. a monomodal flood pulse (Junk et al. 1989; Junk and Wantzen 2004). Due to the distance of the SSLs to the active river channel (Orinoco-Llanos: 2,200–4,000 m, Pantanal: 3,300–9,000 m), the inundation is mainly caused by floodwater resulting from rainfall and by back flooding from the river main stem, rather than from direct bank overflow. Consequently, drawdown is caused by a mixture of evapotranspiration; drain and groundwater recharge (Girard and Nunes da Cunha 1999). Large floods at an approximately decennial frequency, however, may directly connect the SSLs to the main channel of the river. While for the Pantanal some information is available about the impact of the flood pulse on water quality and plant growth (Heckman 1994; Lemes do Prado et al. 1994; Penha et al. 1999), for the Orinoco floodplain only very few data are available from Venezuela (Hamilton and Lewis 1990).

We worked on several SSLs from the Colombian Orinoco-Llanos and the Brazilian Pantanal. The first study area, in the Orinoco-Llanos, is located in the floodplain of the Cusiana

river at the municipalities of Tauramena and Mani ($4^{\circ}49.968'N$, $72^{\circ}26.793'W$ – $4^{\circ}52.652'N$, $72^{\circ}32.261'W$) (Fig. 1). Here, SSLs are locally known as *esteros*. The second study area, in the Pantanal, is located in the sub region of Poconé, on the floodplain of Piraim river (Paraguay river basin) at the field station of the Federal University of Mato Grosso (UFMT) and nearby ranches ($16^{\circ}19.255'S$, $56^{\circ}20.817'W$ – $16^{\circ}22.834'S$, $56^{\circ}19.591'W$) (Fig. 1). In this region, the studied SSLs are locally known as *vazantes*. Both seasonal savannah floodplains have similar rainfall and hydrographs (Fig. 2), showing well defined flooded and non-flooded seasons. However, these occur in opposite order, i.e. when the non-flooded season takes place in the Orinoco-Llanos, it is flooded season in the Pantanal (Fig. 2).

Experimental Design and Sampling

We carried out field-work in ten SSLs, five from each study area, during flooded and non-flooded seasons, in both areas and sampling mostly after peak season. Flooded season samplings were carried out when drawdown had already started, as we expected to have an accumulation of organic matter (OM) inputs into the sediment, related to plant biomass as a result of the end of the growing season (Fig. 2) (Pantanal: 21.04.2010–5.05.2010; Orinoco-Llanos: 4.11.2010–4.12.2010). Non-flooded season samplings were performed at the middle and end of the non-flooded season in the Orinoco-Llanos (24.02.2011–14.03.2011) and the Pantanal (10.12.2010–24.12.2010), respectively (Fig. 2). The sampling was done along two transects per SSL. Aerial photographs and field measurements were used to determine the transverse distance (distance perpendicular to the longest axis) of each SSL (Fig. 3). The transverse distance was divided into seven strips of equal width, parallel to the longest SSL axis. We then used the six internal strip margins as transects. Two of these six transects were randomly chosen for sampling, using a die. We sampled in every lake, keeping the same direction and taking care to avoid disturbing sampling areas for the subsequent sampling events. To evaluate temporal changes, we kept the same sampling points along the two seasons in both study areas (Greenwood and Robinson 2006). Every 60 m, we registered geographical position, water depth, and took biomass and sediment samples.

Biomass Assessment and Sediment Composition

We quantified vegetal biomass (green and dead plants) as the principal organic carbon source, and organic carbon concentration in soil as a potential carbon sink. Tree litter was not considered here, as it is of minor importance in these open (unforested) savannah floodplains. The biomass and sediment samples were composed of three subsamples respectively, which were taken approximately at the angles of a 1 m side

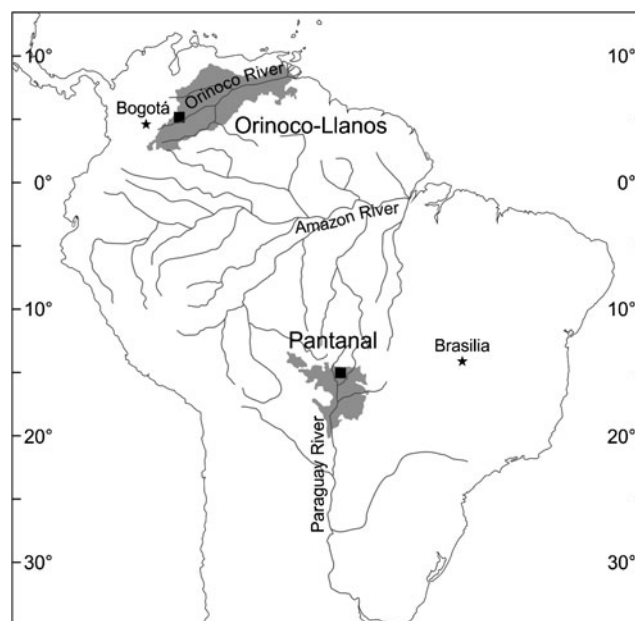


Fig. 1 Map of the study areas. *Black square* = Location of the studied seasonal shallow lakes in the Orinoco-Llanos ($4^{\circ}49.968'N$, $72^{\circ}26.793'W$ – $4^{\circ}52.652'N$, $72^{\circ}32.261'W$) and the Pantanal ($16^{\circ}19.255'S$, $56^{\circ}20.817'W$ – $16^{\circ}22.834'S$, $56^{\circ}19.591'W$)

triangle (Fig. 3). Biomass subsamples were removed, covering an area of 324 cm^2 with a tube corer and cutting biomass with the aid of a knife, approximately at ground level (Bullock 2006), as in flooded season the bottom sediment in SSLs is very soft. Sediment subsamples were taken, using a cylindrical metallic sampler ($\varnothing 4.6\text{ cm}$), to a depth of 15 cm. Both types of sample were packed and transported in labeled plastic bags. Every season, 91 and 65 samples of biomass and sediment were taken in SSLs from the Orinoco-Llanos and the Pantanal respectively, giving a total of 312 samples, each composed of three subsamples.

At the laboratory, biomass samples composed of roots, green and decomposing plants, were washed and dried in a ventilated oven at $60\text{ }^{\circ}\text{C}$ to constant weight. The total biomass dry weight per sampling point was recorded. At the same time, sediment subsamples were mixed and plant parts larger than 2 mm diameter (roots, debris etc.) were removed by hand and discarded in order to avoid reading errors in the carbon analyser. The small roots remaining in the sediment which are predominant in floodable savannahs (Barbosa et al. 2012), can be taken as part of the soil organic matter, in accordance with the IPCC (2006). Sediment samples were then dried in a ventilated oven at $60\text{ }^{\circ}\text{C}$ to constant weight. Dry sediment was ground and passed through a $125\text{ }\mu\text{m}$ stainless steel sieve. The fine sediment portion was weighed and used to calculate carbon and nitrogen contents (%), with a CarloErba Elemental Analyzer CHN-1110 (Milan, Italy) at the Isotope Ecology lab of the CENA-USP, Centro de Energia Nuclear na Agricultura -Nuclear Research Centre in Agriculture–São

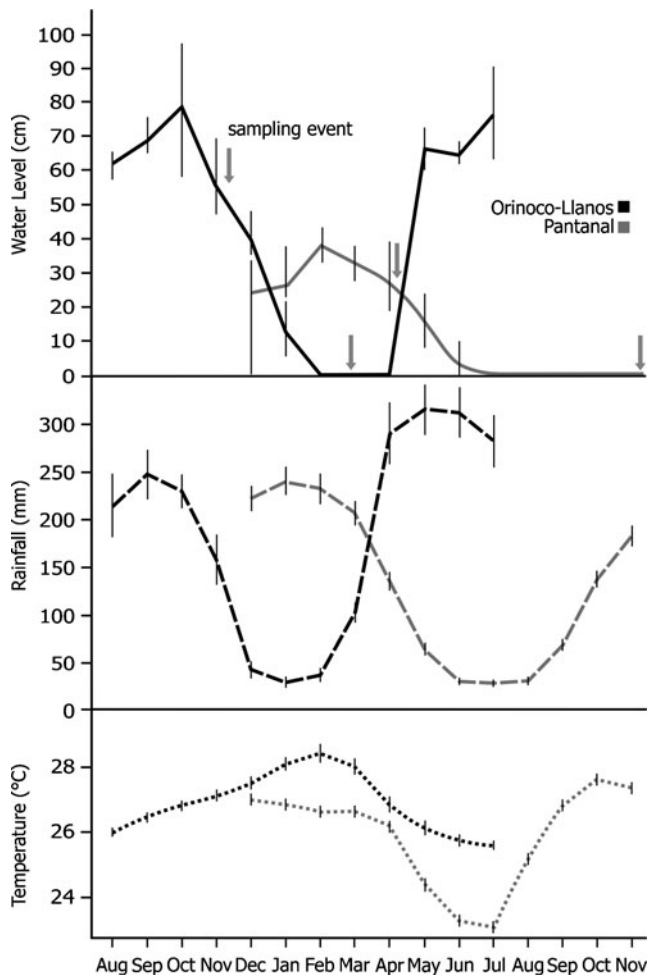


Fig. 2 Flood pulse, rainfall and temperature of the Orinoco-Llanos and the Pantanal. Flood pulse of a seasonal shallow lake from Orinoco-Llanos (2010–2012) and from Pantanal (2007–2010, data adapted from Fantin-Cruz et al. 2010). The arrows indicate the sampling events. Rainfall and temperature of the Pantanal (1961–2010) at the Principal Climatological Station of Cuiaba, Mato Grosso (15°37'S, 56°06'W) (INMET, Instituto Nacional de Meteorologia–Meteorological National Institute), Brazil. Rainfall and temperature of the Orinoco-Llanos (1993–2012) at the Tamarindo Climatological Station (05°01'N, 72°33'W) and the Aguazul Climatological Station (05°10'N, 72°33'W), respectively (IDEAM, Instituto de Hidrología, Meteorología y Estudios Ambientales—Institute of Hydrology, Meteorology and Environmental Studies), Colombia

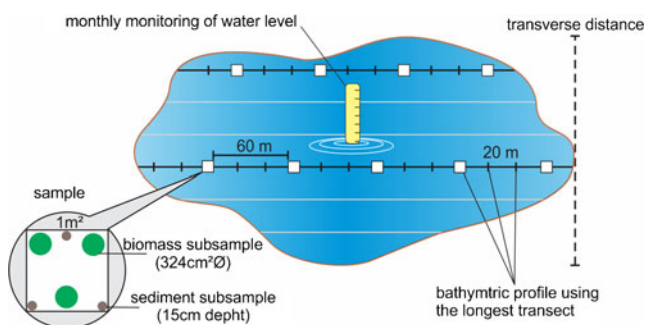


Fig. 3 Sampling design illustration

Paulo University, Piracicaba, Sao Paulo State, Brazil. Carbon storage in SSLs was estimated, computing SOC content, sediment density and depth of the sampled sediment. Sediment density values from Pantanal were estimated from Novaes Filho (2012).

Bathymetry

During the flooded season, a bathymetric profile of the ten SSLs was made, using the longer of the two sampling transects, along which we registered geographical position and water depth every 20 m.

Flood Pulse

In the SSLs from Orinoco-Llanos, we established a monitoring site, where water level was registered monthly. In the Pantanal, part of the study area is located in a 25 km² Ecological Long-Term Research Site (Site #12 of the Brazilian LTER program PELD). Within this program, the water level is registered at least twice per month. We used the water level monitoring to calculate the water level variation rate per month and day. Then, we computed it with the depth of each point from the sampling events to obtain the inundation days/year at every sampling point. The information about rainfall and temperature of the Pantanal (from 1961 to 2010) was taken from the Principal Climatological Station of Cuiaba, Mato Grosso (15°37'S, 56°06'W); INMET, Instituto Nacional de Meteorologia–Meteorological National Institute, Brazil. In the Orinoco-Llanos, the information about rainfall and temperature (from 1993 to 2012) was taken from the Tamarindo Climatological Station (05°01'N, 72°33'W) and the Aguazul Climatological Station (05°10'N, 72°33'W), respectively; provided by IDEAM, Instituto de Hidrología, Meteorología y Estudios Ambientales–Institute of Hydrology, Meteorology and Environmental Studies, Colombia.

Statistical Analyses

We used a linear mixed effect model (Crawley 2007; Zuur et al. 2009) to test the significance of flooded days, biomass, and the interaction of these two variables to explain the SOC storage dynamic in SSLs. The model took into account the random effect of each SSL on SOC and the variance heterogeneity of the data. As carbon results are presented as a proportion of soil, their values were arc-sine transformed in the model. Additionally, we applied a Wilcoxon test to determine the significance of the difference between study area comparison of flooded days, rainfall and temperature, and between-seasons and study area comparisons of SOC and sediment nitrogen percentage and biomass. Using this test, we also verified if the seasonal differences (non-flooded season minus flooded season) of SOC from Orinoco-Llanos and Pantanal were significantly different from zero.

Finally, to assess the relationship between SOC and sediment nitrogen contents, we performed a linear regression analysis. Data analysis was conducted using the ‘R’ program (R Development Core Team 2013).

Results

Hydrography and Morphology

Even though great effort was taken to choose the SSLs from Orinoco-Llanos and Pantanal to be as similar as possible considering their vegetation and landscape settings, some hydrographic patterns varied between the two areas. The flood pulses of SSLs from both systems, showed monomodal patterns, but they differed in seasonal length (Fig. 2). Flooded (filling, full and draw-down) and non-flooded seasons in the Orinoco-Llanos lasted approximately ten (from April to January) and two months (February and March), respectively. The flooded season in these SSLs started in April-May, two months later after the beginning of the rainy season in February-March. In the Pantanal, the non-flooded season covered nearly half of a year (from July to November). Here, the flooded season started in November-December, three months after the beginning of the rainy season in August-September. The number of flooded days varied between 224 and 365 and 58–298 days for the Orinoco-Llanos and Pantanal SSLs, respectively, and the difference between the two systems overall was significant (p -value<0.001). In the SSLs from the Orinoco-Llanos, several sampling points kept some water around the whole year, while in the Pantanal all sampling points dried up during non-flooded season (depending on annual and multi-annual non-flooded season intensity). The rainfall and temperature were significantly higher in the Orinoco-Llanos than in Pantanal (p -value<0.001 and p -value<0.001, respectively). It is interesting that during the driest months of the year, Orinoco-Llanos and Pantanal experience their hottest and coldest mean temperature, respectively (Fig. 2).

The studied SSLs from Orinoco-Llanos had a more elongated shape than SSLs from Pantanal, which were more rounded. In the Orinoco-Llanos, SSLs were deeper and showed better defined contours in the lake margins. In contrast, the SSLs from the Pantanal were shallower and their borders sometimes merged with the surrounding flooded meadows during the flooded season (Fig. 4).

Sediment Organic Carbon, Biomass and Nitrogen

The linear mixed effect model showed that SOC storage in SSLs was significantly explained by the number of flooded days in both regions (p -value = 0.0057) (Fig. 5a). The seasonal mean of SOC increased when the number of flooded days was higher. The SSLs from Pantanal had lower numbers of flooded days in comparison with SSLs from the Orinoco-

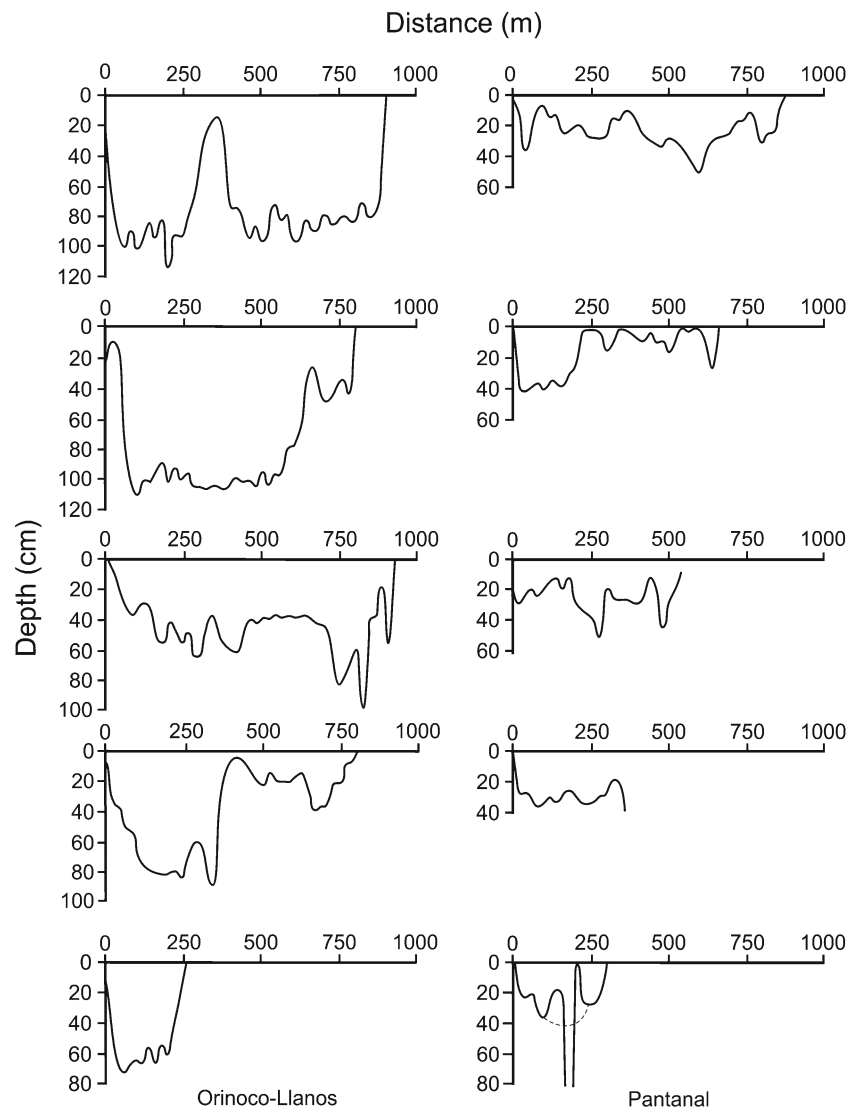
Llanos. Therefore the seasonal mean percentage of SOC storage in SSLs from Pantanal was smaller than in SSLs from the Orinoco-Llanos. On the other hand, biomass and the interaction between biomass and flooded days were not significant (p -value=0.4231, p -value= 0.2826, respectively). The seasonal differences of SOC (non-flooded season minus flooded season values) showed a tendency for accumulation of SOC in SSLs from Orinoco-Llanos and mineralization in the Pantanal, respectively (Fig. 5b). However, the mean values of the seasonal differences of SOC from the Orinoco-Llanos and the Pantanal were not significantly different from zero (p -value=0.3864, p -value=0.407, respectively).

The sediment nitrogen displayed a similar variation pattern to SOC and biomass (Fig. 6). From the flooded to non-flooded season in the Orinoco-Llanos, all these parameters showed a significant increase, while in the Pantanal they declined significantly. SOC, nitrogen, and biomass of SSLs from the Orinoco-Llanos were significantly higher than in SSLs from the Pantanal in all season comparisons (Fig. 6, Table 1). Sediment nitrogen content showed a high correlation with SOC, in SSLs from Orinoco-Llanos and Pantanal and across seasons (Orinoco-Llanos: flooded season, $R^2=0.9453$; non-flooded season, $R^2=0.8895$. Pantanal: flooded season, $R^2=0.9153$; non-flooded season, $R^2=0.9618$).

Discussion

Seasonal water level fluctuation is a common characteristic of most wetlands (Reddy and DeLaune 2008; Wantzen et al. 2008b; Adhikari et al. 2009). In SSLs water fluctuation is remarkable as they experience reiterative dry periods, which gives them some characteristics of temporary water bodies (Williams 2006). The hydroperiod of these water bodies is defined by an annual flood pulse. In SSLs from both the Orinoco-Llanos and the Pantanal, it is caused primarily by rain and runoff water, according to our field observations. The differences of the flood pulse patterns from both study areas (Fig. 2) are mainly due to differences in SSL geomorphology (Fig. 4). The SSLs from the Orinoco-Llanos are more concave, being able to keep water for longer periods in comparison to the SSLs from the Pantanal. Additionally, the filling of SSLs in the Orinoco-Llanos takes place a month faster than for SSLs in the Pantanal in relation with the beginning of the rainy season (Fig. 2). This can be explained by the interaction between a fast increase of rainfall in the Orinoco-Llanos and a dryer soil in SSLs from Pantanal. At the beginning of the rainy season, the rainfall in the Orinoco-Llanos increases from 20.98 ± 7.27 to 273.98 ± 31.93 mm, from February to April, while in the Pantanal it increases from 14.92 ± 4.04 to 121.41 ± 8.67 mm, from August to October. Based on these rainfall data, and the fact that in the Pantanal the non-flooded season is longer (see below) and its soils have a sandier composition in

Fig. 4 Bathymetric profiles of the seasonal shallow lakes (SSLs) from the Orinoco-Llanos and the Pantanal. The last SSL from the Pantanal has an artificial excavation. The dotted line is an approximation to its original bathymetric profile



the horizon A(Couto and Oliveira 2011; Alho and Sabino 2012), we assume that soils from the Pantanal are generally

drier and therefore more intensively oxygenated than those in the Orinoco-Llanos.

Fig. 5 **a** Seasonal mean of sediment organic carbon (SOC) grouped by seasonal shallow lake (SSL) and **(b)** seasonal difference of SOC (non-flooded season minus flooded season), according to flooded days/year per sampling point. SSLs from Pantanal are represented with open symbols and SSLs from Orinoco-Llanos with full symbols. The bars indicate standard deviation

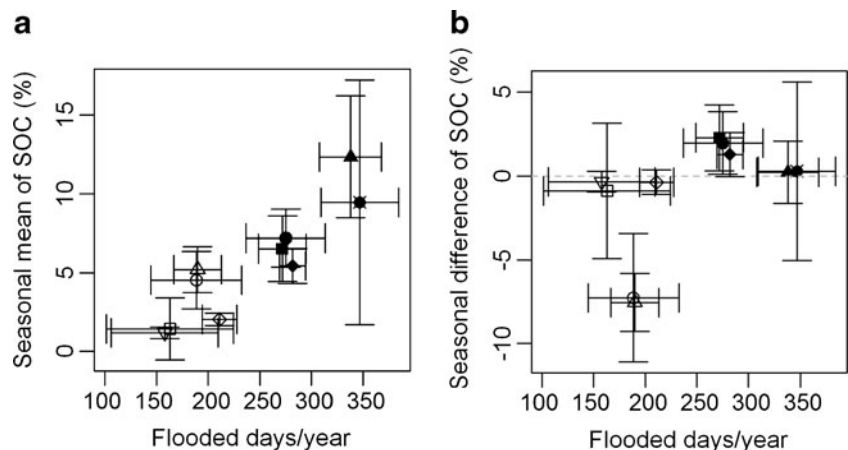
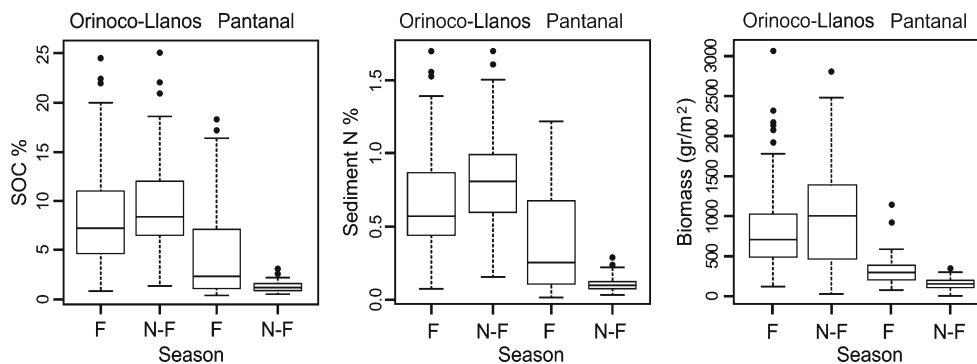


Fig. 6 Sediment organic carbon (SOC) and nitrogen percentages and plant biomass of seasonal shallow lakes by study areas and seasons. The median, quartiles, 1.5 interquartile range and outliers are indicated. F = Flooded season, N-F = Non-flooded season



The number of flooded days of SSLs from the Orinoco-Llanos (307.38 ± 46.15) was significantly greater than SSLs from the Pantanal (177.87 ± 49.93). The amount of biomass was also significantly greater in SSLs from the Orinoco-Llanos than from the Pantanal (Fig. 6, Table 1). The significant rise of SOC storage in SSLs from the Orinoco-Llanos was driven by the number of flooded days (p -value=0.0057), rather than by the amount of biomass (p -value=0.4231) or the interaction between these two variables (p -value=0.2826, Fig. 6, Table 1). The longer flooded season of SSLs from the Orinoco-Llanos in comparison with SSLs from the Pantanal (Fig. 2) had a significant effect on SOC storage. Although the oxygen content in the sediments was not measured in this study, it is well documented that OM decomposition is slow under flooded anaerobic conditions prevailing in wetted lake sediments (Moore and Dalva 1997; Zhang et al. 2002; Johnson et al. 2013). On the other hand, periodic drying leads to aeration and quick decomposition of deposited OM, resulting in carbon stock losses (Mitra et al. 2005; Mitsch et al. 2010). This process is critical in the Tropics, as the high temperature increases metabolic rates of microorganisms (Price and Sowers 2004). Therefore, variation in the length of flooded and non-flooded seasons (flood pulse pattern) among SSLs can strongly influence their capacity to store carbon (Fig. 5), which has also been observed in other types of wetlands (Zhang et al. 2002; Reddy and DeLaune 2008). However, carbon mineralization can be also influenced by

other factors different from an/aerobic conditions; such as carbon speciation, redox, soil texture and microorganism activity (Schwendenmann et al. 2007; Hamarashid et al. 2010).

The SSLs from the Pantanal are able to increase their carbon stock in the flooded season, when aquatic macrophyte production is high (Penha et al. 1999) and runoff water can transport allochthonous OM to them. During the flooded season, the sediment carbon percentage was significantly higher than in the extensive non-flooded season (Fig. 6, Table 1), when OM becomes aerated and decomposed. In contrast, in SSLs from the Orinoco-Llanos, SOC was significantly higher in the non-flooded season than in the flooded season (Fig. 6, Table 1). This can be explained by living (autochthonous) and dead (autochthonous and allochthonous) plant biomass (as a carbon source) that are maintained in the water column during flooded season. Later, during the draw-down period, the falling water level causes aquatic plant decay and increases autochthonous and allochthonous OM accumulation in the remaining shallow water and wetted sediments (Vega et al. unpublished manuscript). In the flooded season, the predominant vegetation among the SSLs is rooted aquatic macrophytes, which remain at their sites when water levels fall and can also act as traps for allochthonous OM (Vega et al. unpublished manuscript). From the carbon storage dynamics in the Pantanal, we assumed that some portion of the stored carbon in SSLs from the Orinoco-Llanos could be lost due to decomposition at the end of non-flooded season. The variation

Table 1 Significance of the difference between-seasons and study area comparisons (Wilcoxon test) for sediment organic carbon (SOC) %, sediment nitrogen (N) % and biomass

Study area and season	SOC %			Sediment N %			Biomass (gr/m ²)		
	Lla F	Lla N-F	Pan F	Lla F	Lla N-F	Pan F	Lla F	Lla N-F	Pan F
Lla N-F	0.011			0.001			0.034		
Pan F	0.000	0.000		0.000	0.000		0.000	0.000	
Pan N-F	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Lla Orinoco-Llanos, Pan Pantanal, F flooded season, N-F non-flooded season

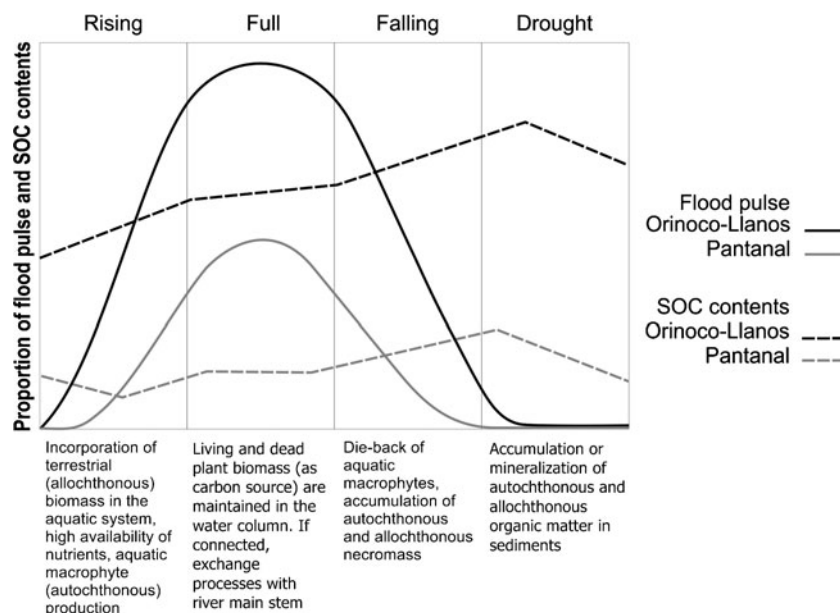
in length of the non-flooded season in SSLs, being shorter in the Orinoco-Llanos and longer in the Pantanal, tends to promote an accumulation and mineralization of SOC, respectively (Fig. 5b). However, the seasonal differences of SOC from the Orinoco-Llanos and the Pantanal were not significantly different from zero (p -value=0.4074, p -value=0.3864, respectively).

Due to the large distance between sampling areas, the experimental setup of our study did not allow for a higher sampling frequency of the sediments. However, from field observations and previous studies, we can infer some elements of the dynamics of particulate carbon bound in the sediments of the SSLs in both areas (Fig. 7). We suggest that there is an accumulation of SOC at the beginning of the non-flooded season in both areas. This carbon comes from autochthonous and allochthonous sources. The autochthonous carbon is coming from accumulation of OM deriving from aquatic macrophytes that become stranded or partially decomposed, leaving their carbon to integrate into the sediments. The allochthonous carbon is coming from terrestrial plants, especially C4 grasses that have been incorporated into the aquatic system by runoff water during the flooded season, and can make an important carbon contribution (Vega et al. unpublished manuscript). This statement is supported by the study of Nogueira et al. (2002) from a similar area located at a distance of 20 km from our study site in the Pantanal. They found a carbon increase in the sediment samples taken at the beginning of the non-flooded season in July, in comparison to the flooded season samples taken in April (as in our study). At the beginning of the non-flooded season, more than 90 % of their study area had higher OM content than in the flooded season. In the same way, in the Murrumbidgee River floodplain an increase of OM after flood recession was found, in comparison with flooded areas or areas that had not been flooded for a long time (Baldwin et al. 2013). In the latter study, the authors proposed a reciprocal provisioning model as an extension of the flood pulse concept (Junk et al. 1989; Junk and Wantzen 2004). This model proposes that fixed terrestrial carbon will provision the system during the flooded season, and then aquatic macrophyte production will sustain the system during the non-flooded season, even subsidizing other terrestrial components (Baldwin et al. 2013). The reciprocal provisioning model supports some of the SOC dynamics we observed and suggested for SSLs from Orinoco-Llanos and Pantanal. However, in contrast to this model, we attribute the carbon increase after flood recession to a combination of allochthonous and autochthonous OM inputs in sediment of SSLs from Orinoco-Llanos and Pantanal (Vega et al. unpublished manuscript) rather than only to aquatic macrophyte production. We also expect an increase of carbon input at the beginning of the flooded season in SSLs, because the biomass of terrestrial plants growing in SSL depressions is drowned and incorporated into the aquatic system. Additionally, allochthonous OM accumulated during

the previous non-flooded season in SSL basins may be transported into the lakes by surface runoff water, where it can be maintained due to slow decomposition under anaerobic conditions, during the flooded season. Thus, the flood pulse is related not only to SOC storage capacity, but also to organic carbon inputs into SSLs. During our study, none of the lakes became connected to the river main stem; therefore the origins of the floodwater were mainly rain and surface runoff. In previous field studies, where the flood pulse of lakes was caused by the river, we also observed that river dynamics may mobilize and transport large amounts of OM-rich sediments (Wantzen et al. 2005). It is likely that SSLs present a differential carbon dynamics pattern due to their individual flood pulse pattern, connectivity, geomorphology, and biomass accumulation in their basin. In general, it is predictable that OM input in SSLs from the Pantanal is less pronounced (Fig. 7), as they have a less concave morphology, a lower amount of biomass, and a longer drought phase than the SSLs in the Orinoco-Llanos. We suggest that SOC storage of studied SSLs from the Pantanal restarts again every year during the flooded season, whereas SSLs from the Orinoco-Llanos keeps some carbon at the end of non-flooded season, resulting in a more gradual annual carbon sequestration (Fig. 7). Long term monitoring with shorter sampling intervals and detailed analysis of carbon sources will improve our understanding of SOC budget dynamic in SSLs.

The Pantanal and the floodable Orinoco-Llanos plains were originated by sediment deposition during the Pleistocene (Botero and Lopez 1982; Irion et al. 2011). However, the Pantanal is predominately sandy (Couto and Oliveira 2011; Alho and Sabino 2012), while the floodable Orinoco-Llanos have a higher clay and silt content, which derives from the Andes and the higher sections of the Orinoco-Llanos (Botero and Lopez 1982). This difference in sediment composition is may be another factor that can influence SOC storage in SSLs. Clay and silt can be nutrient repositories due to their cation exchange capacity and so increase plant growth in the flooded season in SSLs of the Orinoco-Llanos. The presence of clay has also been associated with soil carbon content in many studies (see Wantzen et al. (2012) for further citations). In areas with elevated OM input and sediments rich in clay, Al, Fe and carbonates, high humification and its resulting high carbon contents are common (Woomer et al. 1994). During the non-flooded season in SSLs from Pantanal, sandy sediments will become drier and better aerated, which speeds up decay of organic matter. Additionally, SSL morphology is also related to sediment transport, retention, and consequently sediment composition. The more concave shape of SSLs from the Orinoco-Llanos could permit longer water retention times, facilitating fine particles (such as clay) and carbon input and deposition. In contrast, clay and carbon are presumably not retained for long in SSLs from the Pantanal, since they have a more open and shallow morphology with more flow

Fig. 7 Model of flood pulse (Flood Pulse Concept (Junk et al. 1989)) and sediment organic carbon (SOC) dynamics in Orinoco-Llanos and Pantanal. In the Orinoco-Llanos, due to a short drought phase, autochthonous and allochthonous carbon is only partly mineralized; a larger part becomes accumulated into sediment. In the Pantanal, during the long drought phase this carbon becomes mostly mineralized



connections to other water bodies during the flooded season. The amount of SOC increases nutrient availability as OM is a reservoir of nitrogen and other nutrients (Reddy and DeLaune 2008). This was corroborated from the high correlations we found between SOC and nitrogen contents across the seasons in the studied areas. In general, SOC, sediment nitrogen, and biomass showed similar fluctuation patterns between seasons and study areas (Fig. 6).

Our study has shown that Neotropical SSLs have a considerable potential for carbon storage. In the limited area of our study in the Orinoco-Llanos, the SSLs cover 119.04 ha (7.32 %) of a 1625.53 ha large study area. There, they have a storage of 107.64–91.32 tonC/ha SSL surface for the upper 15 cm of sediment, during the non-flooded and flooded seasons respectively. In the Pantanal, the SSLs cover 117.68 ha (4.10 %) of a 2866.67 ha large study area, having storage of 23.62–103.53 tonC/ha SSL surface, during the non-flooded and flooded seasons respectively. Even though the average capacity of SSLs from the Pantanal was smaller, it is still considerably high. In both study areas, we have included only the area of the studied SSLs. However, there are several SSLs and other wetlands in each study area.

The strong reduction of the C storage in SSLs from the Pantanal compared to the Orinoco-Llanos can be attributed to its long non-flooded season. This study points out the SSL sensitivity to climate change effects, such as higher temperature, reduced or retarded rain periods, or extended non-flooded seasons, which may have a decisive effect on whether a shallow lake keeps a residual water layer and humid soil or not, and thus on its carbon storage potential. In a global warming scenario, the SSLs from the Orinoco-Llanos and other SSLs with similar SOC dynamics would be strongly

affected, if their non-flooded season was expanded. This is supported by previous reports from other wetland studies (Gorham 1995; Keddy et al. 2009; Mitsch et al. 2010).

Apart from climate change, human activities may modify morphology, flood pulse, and vegetation and thus, carbon storage capacity. These SSL features are transformed with agrarian border expansions, which normally involve vegetation cover substitution and the installation of irrigation and draining systems. Many of these processes have been encouraged by governments, due to the often classical view that wetlands are wastelands (Mitra et al. 2005). This is the case with the Colombian Orinoco-Llanos, which are facing land use changes ranging from extensive cattle ranching to rice and oil palm crops, among others (Regional Competitiveness Commission 2010).

If data from both regions are viewed synoptically (Fig. 5b), there seems to be a critical threshold between “non-flooded season losses” and “non-flooded season storage” of SOC in a range of 225–275 flooded days per year. Considering imminent changes in the hydrological regime of SSLs in the Neotropics and worldwide in the Tropics, due to increasing land use changes for agricultural purposes and climate change, we suggest further analysis and careful management of the ‘carbon storage/release-switch’ in order to avoid further massive carbon releases to the atmosphere.

Apart from carbon storage, wetlands offer important and essential environmental services and goods to human populations including water storage, treatment and supply, flood regulation, biodiversity support, and elemental cycling (Mitra et al. 2005; Barker and Maltby 2009; Keddy et al. 2009; Russi et al. 2013). Nowadays, wetlands are considered as some of the most productive ecosystems on the planet, also

being able to subsidize terrestrial ecosystems. The high productivity of seasonal wetlands (Junk and Wantzen 2004) including SSLs, supports the production of cattle, horses, deer, capybaras (Escobar and Gonzalez-Jimenez 1976), wild pigs, caimans (Junk and Nunes da Cunha 2012) and kangaroos (Baldwin et al. 2013). All of these ecosystem services may be integrated into sustainable management concepts (e.g., Wantzen et al. 2008a) that profit from the traditional management schemes that have been developed over centuries. Carbon storage may deliver an important argument for the preservation of wetlands, especially in the Tropics (Mitsch et al. 2012), as they “are probably the best ecosystem on the planet to sequester carbon” (W. Mitsch 2009 in (Lenart 2009)).

Acknowledgments This research was partially supported by National Institute for Science and Technology of Wetlands (INCT-INAU), Brazil, German Academic Exchange Service (DAAD), State Law on Graduate Funding (LGFG), Germany, the Carbiocial project (www.carbiocial.de) and Idea Wild. We would like to thank the Pantanal Research Centre (CPP) and National Institute for Science and Technology of Wetlands (INCT-INAU) in Brazil, and Las Aguilas Ranch, Educational Institute of Cusiana (IEC) and University of Tropic, Casanare, in Colombia, for their logistical support. We express our gratitude to all field and laboratory assistants involved in this work, especially Abilio Moraes, Thayse M. Marestoni, and Sejana Arteaga in Brazil, and Ricardo Sá, Vicente Preciado, Ginna Cruz, Lukas de Ventura and Jennifer Ardila in Colombia. We thank a number of ranches: Retiro Novo, Aparecida, Oreana, and Paulo das Canoas in Brazil, and Cuernavaca, Arizona and Flor Amarillo in Colombia. We also thank Diego Orduz for kindly assisting us with designing illustrations and Luisa F. Ricaurte for her comments on the manuscript. Paper #2 of the UNESCO Chair on River Culture/Fleuve et Patrimoine.

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