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Macrophytes and groundwater drive extremely high organic carbon concentration of soda pans

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Abstract

1. Endorheic soda pans are among the highest dissolved organic carbon (DOC) content aquatic systems on the planet with concentrations up to 1 g/L. Considering the importance of inland waters in the global carbon cycle, understanding the drivers of such outstanding organic carbon pools is eminent. The soda pans of the Carpathian Basin present a wide variability of biotic and abiotic characteristics that provide an adequate system to assess the determinants of extreme high DOC concentrations. Here, we demonstrate through a multi-site comparison, a multi-year seasonal monitoring, and a laboratory experiment that the dissolved organic matter content of the highest DOC concentration soda pans is primarily of groundwater and emergent macrophyte origin.
2. More precisely, the multi-site comparison of 14 soda pans revealed that variation of coloured dissolved organic matter (CDOM) content of the surface water of soda pans is partially explained by the CDOM content (22% of variation) of local groundwater, indicating the significant role of allochthonous terrestrial DOC sources. Further 23% of CDOM variation could be accounted for by *Bolboschoenus maritimus* species-specific emergent macrophyte cover, while the contribution of *Phragmites australis* cover was only minor.
3. In line with the results of the multi-site comparison, our decomposition experiment demonstrated that both *B. maritimus* and *P. australis* have the potential to release substantial amount of organic matter into soda pans. However, the organic matter release of *B. maritimus* leads to twice as high DOC and 3.5-times higher CDOM concentrations than *P. australis*. Considering previous organic matter release studies, we concluded that *P. australis* is a relatively low organic matter releaser emergent macrophyte, and therefore the species composition of emergent macrophytes has to be carefully considered in autochthonous plant-derived DOM estimations.
4. Finally, the multi-year seasonal monitoring of two distinctive soda pans showed that the high organic matter concentrations depend not only on their intrinsic characteristics but also on interannual variability. More precisely, we demonstrated that the highest CDOM and DOC concentrations that occurred in a coloured (i.e. brown, low total suspended solids) soda pan with extensive (95%) macrophyte cover dominated by *B. maritimus* were measured in a period characterised by high

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pH and low water levels, which were presumably the consequence of increased evaporation due to decreased precipitation and above average temperature.

5. Our results indicate that considering climate change trends common for most endorheic regions (i.e. increased temperature and modified precipitation regimes), extremely high organic matter concentrations might become more frequent in the near future in local water bodies, particularly in those highly influenced by groundwater inflow. Furthermore, soda pans with vast specific macrophyte cover and substantial groundwater inflow might become organic carbon processing hotspots.

KEYWORDS

dissolved organic matter , emergent macrophytes, groundwater effect, high pH, interannual variability

1 | INTRODUCTION

As inland waters receive, process, store, and emit carbon in globally significant amounts (Cole et al., 2007), mapping active carbon in even the smallest aquatic systems is necessary for accurate global estimates of carbon cycling (Tranvik, Cole, & Prairie, 2018). Dissolved organic matter (DOM) is quantitatively the most significant pool of organic carbon in aquatic systems, which is either derived from terrestrial sources (i.e. allochthonous) or from biological material produced in situ by phytoplankton and macrophytes (i.e. autochthonous) (Williamson, Morris, Pace, & Olson, 1999; Zhang, Liu, Wang, & Qin, 2013). Terrestrial DOM can reach surface waters via surface inflow or runoff as well as via groundwater seepage (Einarsdottir, Wallin, & Sobek, 2017; Grabs, Bishop, Laudon, Lyon, & Seibert, 2012; Wetzel, 2001). Therefore, the quantity and quality of DOM in inland waters is not only influenced by internal processes but also by the characteristics of the catchment area (e.g. vegetation, soil type, hydrology; Kothawala et al., 2014; Sepp, Kõiv, Nõges, & Nõges, 2019; Wetzel, 2001).

In inland waters, DOM is considered to be dominated (15–80%) by soluble humic substances (i.e. fulvic acids and humic acids). The pH affects the solubility of humic acids with no dissolution at lower pH (pH < 2) and complete solubility at pH 13 (Aiken, McKnight, Wershaw, & MacCarthy, 1985) and the quality of humic substances as more aromatic and aliphatic compounds dissolve at higher pH (Baglieri, Vindrola, Gennari, & Negre, 2014). Humic substances contribute to the fluorescence signal of coloured (chromophoric) DOM (CDOM) (Lapierre & Frenette, 2009) and their aromatic core makes them relatively resistant to microbial degradation (Kellerman, Kothawala, Dittmar, & Tranvik, 2015). Therefore, the high humic content of allochthonous DOM suggests higher recalcitrance than phytoplankton derived autochthonous DOM (Tranvik, 1988; Wetzel, 2001). However, refractory plant-derived CDOM can also originate from autochthonous sources such as littoral marshland vegetation (i.e. emergent macrophytes) (Lapierre & Frenette, 2009).

The mean of global dissolved organic carbon (DOC) concentration of lakes is 5.02 mg/L (equivalent of 5.58 mg/L total organic carbon) and its variance is influenced by climatic factors (Chen et al., 2015) and catchment characteristics (Sobek, Tranvik, Prairie, Kortelainen, & Cole, 2007). Although the globally most abundant shallow lakes (Downing et al., 2006; Verpoorter, Kutser, Seekell, & Tranvik, 2014) have been shown to have double mean DOC concentration than deep lakes (6.56 and 3.12 mg/L, respectively) (Chen et al., 2015), the 90 mg/L mean DOC concentration of soda lakes can be considered as extreme even among highly productive aquatic systems such as eutrophic lakes, marshes, or bogs (Figure 1a). In addition, some single measurements of soda pans are very likely to represent the world record in DOC concentration as occasionally values close to 1 g/L have been reported (Lake Nakuru: 980 mg/L [Jirsa et al., 2013]; Sósér: 988 mg/L [Boros et al., 2016]) (Figure 1b).

Soda lakes and pans can be found on all continents except Antarctica and represent the most alkaline natural environments on Earth (Grant & Sorokin, 2011). Soda lakes are formed in endorheic basins (i.e. limited drainage basins), where evaporation exceeds water outflow (Warren, 2006) and the levels of calcium (Ca^{2+}) and magnesium (Mg^{2+}) are low, while sodium (Na^{+}) and carbonate species ($HCO_3^- + CO_3^{2-}$) are high (Boros & Kolpakova, 2018). Within Europe—to the best of our knowledge—soda pans are restricted to the Carpathian Basin (Austria, Hungary, and Serbia). The climatic conditions of the region (i.e. continental with influence of both oceanic and Mediterranean climate) in combination with the shallowness of the pans lead to high water level and temperature fluctuations. Water level fluctuation is of particular interest as it often results in intermittent hydroperiods and affects the concentration of both organic and inorganic compounds. In the Carpathian basin soda pans groundwater inflow typically exceeds the surface-related catchment inflow and precipitation (Boros, Ecsedi & Oláh, 2013). Analyses of soda pans in the region showed that many pans have extremely high DOC and CDOM concentrations (DOC: median = 47; range: 20–664 mg/L; CDOM: median = 310; range: 20–7,100 mg Pt/L), indicating polyhumic (CDOM > 90 mg Pt/L) character (Figure 1b) (Boros,

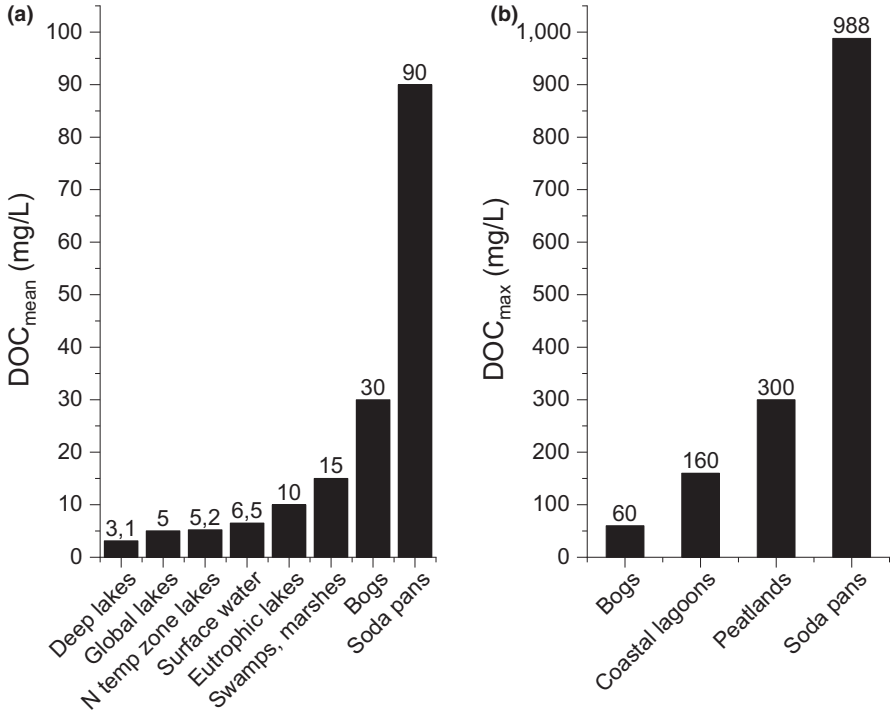


FIGURE 1 Global mean (a) and maximum (b) concentrations of dissolved organic carbon (DOC) in inland waters. Data sources: (Wetzel, 2001) for surface water; (Chen et al., 2015) for lakes; (Thurman, 1985) for lakes, swamps, marshes, bogs; Suhett, Maccord, Amado, Farjalla, & Esteves (2004) for coastal lagoons; (Boros et al., 2013, 2016, 2017) for soda pans. N term zona lakes stands for Northern temperate zone lakes

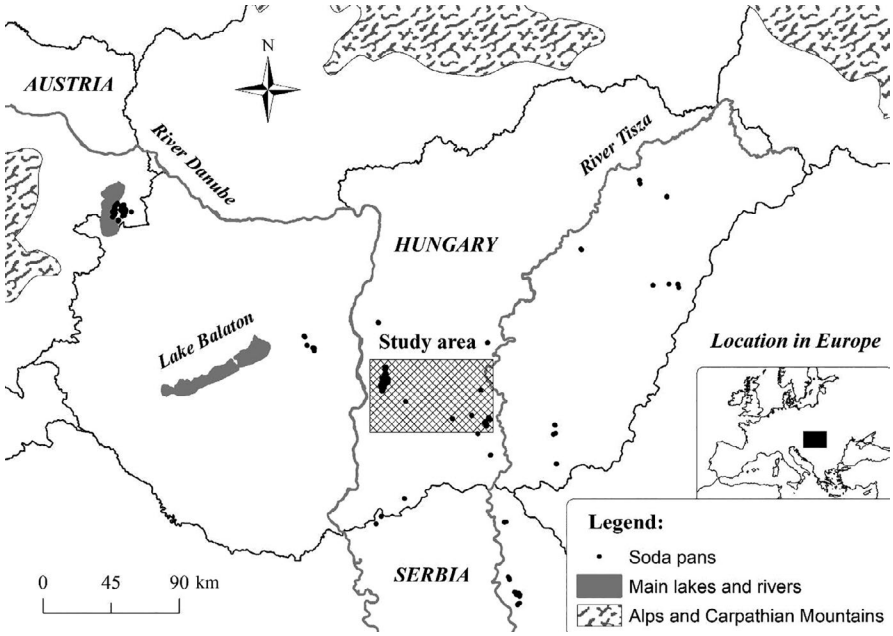


FIGURE 2 Location of studied soda pans within the Carpathian Basin based on Boros et al. (2017)

V.-Balogh, Vörös, & Horváth, 2017) (Boros et al., 2016). Positive correlation between DOC and CDOM has been determined before for Carpathian soda pans (Boros, Ecsedi, & Oláh, 2013; Boros et al., 2016, 2017; V.-Balogh, Németh, & Vörös, 2009), while—despite the pH-dependent solubility of humic substances (Aiken et al., 1985)—correlation between pH and DOC has not been demonstrated on a regional scale (Boros et al., 2017).

Although high organic matter content is an inherent property of most soda pans, the temporal and spatial regulators of CDOM variation across pans are understudied and the causes of extremely high DOC and CDOM concentrations are not properly understood. Therefore, in this study we aim to identify and test the main sources of CDOM and DOC in polyhumic soda pans of the Carpathian basin. Namely, we hypothesise that CDOM concentration of polyhumic soda pans is positively affected by the allochthonous CDOM concentrations of local groundwater and the extent of emergent macrophyte cover. Furthermore, based on our earlier observations (Boros et al., 2017), we hypothesise that the species composition of the autochthonous emergent macrophytes influences CDOM content with cosmopolitan bulrush (*Bolboschoenus maritimus* (L.) Palla, Cyperaceae) cover leading to higher CDOM concentrations than common reed (*Phragmites australis* (Cav.) Trin. ex Steud., Poaceae).

To disentangle the effect of different macrophyte species on CDOM and DOC concentrations, experimental assessment of CDOM and DOC released from *P. australis* and *B. maritimus* was performed. Finally, the drivers of the temporal extremes of DOC and CDOM values of soda pans were identified by seasonal monitoring of a turbid and a coloured polyhumic soda pan in 2 separate years.

2 | METHODS

2.1 | Study sites and sampling

The studied soda pans are located in the central area of the Carpathian Basin, on the interfluve area of the Danube and Tisza rivers (Figure 2). The water budget of these endorheic soda pans is highly influenced by evaporation, precipitation, and groundwater influx, while surface water inflow from the catchment is negligible as usually no major watercourse enters these systems (Boros et al., 2013). The primary source of the high Na–HCO_3–Cl^- content of soda pans in the region is discharge from upwelling deep saline groundwater, which is enhanced by evaporation (Simon, Mádl-Szőnyi, Müller, & Gy, 2011). Based on optical characteristics, these soda pans are categorised into two groups: turbid pans with inorganic suspended solids as the main source of turbidity (i.e. contribution of inorganic suspended solids to light attenuation [K_d] exceeds 50%), and the coloured (brown) pans, where CDOM contribution dominates K_d (>50%) (Boros et al., 2013). Submerged and floating macrophytes are sparse or absent from the open water areas of both turbid and coloured pans. However, marshland vegetation (*Bolboschoeno–Phragmitetum*) characterised primarily by varying ratios of emergent macrophyte species *B. maritimus* and *P. australis* is common on the shoreline. This study comprises of three parts: a multi-site comparison of soda pans, a decomposition experiment, and a seasonal analysis of a turbid and a coloured soda pan.

In the multi-site comparison, 14 natural pans were sampled between April and September of 2017 to assess the potential effect of groundwater and macrophytes on the organic matter content. The pans were selected in order to cover a broad range in respect of turbidity, CDOM and emergent macrophyte cover (Table 1). The coordinates of the location of the pans and the groundwater wells are listed in Table S1. The chemical type of the pans was determined following the guidelines of Boros and Kolpakova (2018). Two of these pans were sampled in the seasonal analysis: Zab-szék, a typical turbid pan (Table 1: total suspended solids [TSS] = 1574 mg/L, CDOM = 364 mg Pt/L) and Sósér, a typical coloured pan (TSS 83 mg/L, CDOM = 2088 mg Pt/L) (Boros et al., 2013, 2016, 2017). The seasonal assessment of these two pans was performed in 2014 and 2017 with sampling approximately every other week from January to December in 2014 and from March to November in 2017. On two occasions in 2017 (11 September and 16 October) Zab-szék was completely dry, so no measurement was possible.

The very shallow (average depth < 0.5 m) polymictic soda pans have relatively uniform flat bottom with only small differences in elevation except for shoreline. Therefore, for each sampling, water depth, conductivity, and pH were measured at a single open water location with water depth representative of the pan using a centimetre-scale pole, and a MultiLine Handheld Meter model 340i with SenTix® 41 electrode for pH and TetraCon® 325 cell for conductivity (WTW, Weilheim in Oberbayern, Germany), respectively. Samples were collected and transported to the lab for CDOM, DOC, TSS, and

TABLE 1 Environmental parameters determined for the soda pans and corresponding groundwater wells in the multi-site comparison

	Soda pan						
Name of pan	Chemical type[a]	Optical type[b]	*B. maritimus* cover (%)	*P. australis* cover (%)	TSS (mg/L)	Electrical conductivity (mS/cm)	pH
Bogárzó	Soda	Turbid	35	9	807	4.97	9.28
Böddi-szék 1	Soda-Saline	Turbid	4	18	745	6.42	9.80
Böddi-szék 2	Soda-Saline	Turbid	0	6	1,100	1.71	9.69
Böddi-szék 3	Soda-Saline	Coloured	0	92	8	1.85	8.39
Büdös-szék	Soda	Turbid	59	0	384	5.23	9.27
Csaba-szék	Soda	Coloured	35	11	50	2.62	8.57
Dongér	Soda-Saline	Turbid	0	13	67	1.63	10.57
Fehér-szék	Soda	Turbid	29	66	585	3.3	8.86
Fülöp-szék	Soda	Coloured	18	64	350	4.09	9.12
Kelemen-szék	Soda	Turbid	25	14	1,850	3.01	9.13
Sósér	Soda	Coloured	57	38	83	8.68	9.89
Unnamed	Soda	Turbid	0	0	692	4.84	9.43
Vesszős-szék	Soda	Turbid	80	0	80	2.05	9.73
Zab-szék	Soda	Turbid	1	16	1574	4.27	9.28

DOM, dissolved organic matter; TSS, total suspended solid.

[ab]Based on Boros and Kolpakova (2018). Based on Boros et al. (2013, 2017).

fluorescence excitation–emission matrix (EEM) spectroscopy (EEMS) measurement. The groundwater was assessed by sampling dug wells (mean depth: 3–5 m) located within 500 m from the shoreline of each pan (Table 1). According to topographic maps, all of the sampled wells were established decades ago. For the macrophyte DOM release experiment, aboveground fraction of stems and leaves of *B. maritimus* and *P. australis* specimens in their early senescing stage were collected from Sósér soda pan in October 2012. After collection, the plant samples were washed with pan water and transported to the laboratory in clean plastic bags.

2.2 | Emergent macrophyte cover assessment

The cover of open water and marshland vegetation of the pans were mapped separately for *P. australis* and *B. maritimus* by RGB raster data of Sentinel 2 MSI sensor from June 2017 (https://landsatlook.usgs.gov/sentinel2/viewer.html) via OpenLayers plugin by visual interpretation and manual screen digitalisation technique. The interpretation of remote sensing sources was controlled by comprehensive field observation of each investigated site. Distinction between the two plant-species was based on the shifts in colour and pattern that occur according to their phenology (i.e. vegetation growth, flowering and senescence) in the middle of growing season (June) when the brownish red colour of flowering *B. maritimus* was clearly distinguishable from the vivid green colour of the fresh foliage of *P. australis*. The GIS mapping procedure and spatial calculations were carried out using ArcMap (Environmental Systems Research Institute 2013). The proportion (%) of *B. maritimus* and *P. australis* cover (Table 1) was summed to calculate the total emergent macrophyte cover of the pans, while the ratio of the two species in the emergent macrophyte was estimated by calculating the ratio (%) of *B. maritimus* within the total emergent macrophyte cover (i.e. *B. maritimus* ratio; Table S2).

2.3 | Experimental release of DOM from macrophytes

Once in the laboratory the plant material was cut into 20-cm-long pieces and oven-dried to constant weight at 35°C to avoid the destruction of the associated microbiome. For each replicate, 50 g of oven-dried plant material (stems and leaves) were weighed and stored at room temperature (23°C). The experiment was performed in March 2013 using fresh well water from the well near Kelemen-szék (Table 1, N: 46.8012; E: 19.1717) to mimic the decomposition processes of the early Spring period. Aliquoted plant material was placed into 5-L bottles containing 3.5 L well-water (pH = 8.4) that was filtered with pre-combusted and acid-washed GF-5 glass fibre filters (pore size = 0.4 μm). The DOC and CDOM concentration of the well water were determined as for other samples. The incubation was performed in three replicates in the dark at room temperature (22–24°C) for 29 days. As an earlier study on *P. australis* showed that aerobic conditions resemble better conditions in the field than anaerobic (V.-Balogh, Présing, Vörös, & Tóth, 2006), the bottles were aerated with sterile-filtered atmospheric air and dissolved oxygen saturation ranged between 64% and 94% throughout the experiment. On days 0, 1, 4, 7, 11, 14, 18, 22, 25, and 29, 100 ml of water were removed from the bottles for analyses and replaced with filtered well water to maintain constant water volume. All glassware used for sample collection

			Groundwater well			
CDOM (Pt mg L^{-1})	Water depth (cm)	Total area (10^4 m^2)	Electrical conductivity (mS/cm)	pH	CDOM (Pt mg L^{-1})	Distance to closest shore of soda pan (m)
1,424	30	34.4	5.46	8.55	107	34
239	9	183.4	2.81	8.83	74	24
253	2	100.6	5.1	9.56	117	16
293	40	29.3	3.4	9.29	303	239
174	12	174.7	2.2	7.73	28	190
1,659	20	24.3	1.86	8.34	841	25
99	20	23.6	0.76	8.64	67	31
684	45	158.3	2.31	8.74	437	155
143	8	29.6	4.01	7.02	28	198
693	20	312.7	1.15	8.15	205	201
2,088	3	64.1	3.54	9.28	69	47
203	20	0.6	1.61	8.73	146	85
282	20	35.2	1.68	8.17	41	467
364	3	174.1	1.05	8.30	667	45

and analytical processes was acid-washed and Milli-Q rinsed. At the end of the experiment, the remaining plant material was oven-dried to constant weight at 35°C and weighed.

2.4 | Coloured dissolved organic matter, DOC, and TSS measurements

The water samples were filtered as for the DOM release experiment and concentration of CDOM was expressed as Pt (platina) units (mg Pt/L) using absorbance (440 nm) measurements (Cuthbert & del Giorgio, 1992) with a UV 160A UV/VIS recording spectrophotometer (Shimadzu). For DOC analyses, the filtered samples were acidified (to pH 2 with HCl) and bubbled to remove dissolved inorganic carbon, and DOC concentration was measured by thermal catalysis at 1,050°C in a high total organic carbon analyser instrument (Elementar) equipped with a platinum cartridge using synthetic air as carrier gas. The concentration of TSS was measured by filtering water (100–2,000 ml) through pre-dried and pre-weighed cellulose acetate filters (pore size = 0.45 µm) followed by oven-drying at 105°C, and weighing of dry filters using an analytical balance (accuracy 0.01 mg, precision 0.02 mg).

2.5 | Fluorescence excitation emission matrix spectroscopy

During the 2017 seasonal comparison of Sósér and Zab-szék samples were collected for DOM characterisation using fluorescence EEMS. The samples were filtered through a 0.1-µm pore size Millipore Isopore Membrane Filters the same day and stored in combusted glassware at 4°C until processing. Excitation–emission matrix spectroscopy profiles of the samples were determined as in Kothawala et al. (2014). Briefly, EEMs were determined by measuring UV-visible absorbance spectra using a Lambda 40 UV-visible spectrophotometer (Perkin Elmer) and measuring fluorescence emission using a fluorescence spectrophotometer (SPEX FluoroMax-2, Horiba Jobin Yvon). Manufacturer supplied instrument correction factors and the measured absorbance spectra were used for the correction of instrument and filter biases, respectively, while fluorescence intensity was calibrated to the Raman area of the blank water (Milli-Q).

2.6 | Data analyses

In the multi-site comparison, to assess the effect of macrophytes on the CDOM content of the pans ($CDOM_{pan}$), the amount of non-groundwater related CDOM ($CDOM_{diff}$) was calculated by subtraction of the CDOM concentration of the corresponding groundwater wells ($CDOM_{groundwater}$) from $CDOM_{pan}$. The potential individual effect of the parameters listed in Table 1 and Table S2 (except the distance of the well to the corresponding pan) on $CDOM_{pan}$ as well as on $CDOM_{diff}$ was assessed by *t*-tests for discrete variables (i.e. chemical and optical type) and by Pearson's correlation analysis for continuous variables. Meanwhile, the combined effect of the different parameters on the $CDOM_{pan}$ was evaluated with linear models. To fulfil the assumptions of independence two candidate models were built: one using the total emerged macrophyte cover and the ratio of *B. maritimus* within the macrophyte cover (model A); and another using the species-specific cover of *B. maritimus* and *P. australis* separately (model B). Correlation among the explanatory variables was inspected in order to avoid high collinearity (Pearson $|r| > 0.7$) (Dormann et al., 2013) (Table S4). Furthermore, to avoid overfitted models, the variables of candidate models A and B were evaluated and selected by backward selection using the *stepAIC* function of R package MASS (Zhang, 2016). The resulting reduced candidate models A and B were compared based on the Akaike information criterion (AIC) and the model that provided the lowest AIC value was considered as the best fit. For the other alternative reduced model, the Akaike-weight was calculated to estimate its relative likelihood and strength compared to the best fit model (Burnham & Anderson, 2002) (Supplementary material and Table S6). The lowest AIC linear model clearly outperformed the alternative reduced model (Akaike weight < 0.001); therefore, it was used to calculate the relative contribution of each variable to the total sum of squares by considering all possible variable orders using the *calc.relimp* function of R package relaimpo. Normality of residuals and variables and homoscedasticity of variables were checked by Shapiro–Wilk test and Levene's test, respectively, and by visual analyses. When needed, the data were log-transformed ($CDOM_{pan}$, $CDOM_{groundwater}$, total area), square-root-transformed ($CDOM_{diff}$) or arcsin-square-root-transformed (*B. maritimus* and *P. australis* cover).

The Spearman correlation, non-linear curve fitting for Michaelis–Menten kinetic function, Mann–Whitney, and Kruskal–Wallis tests used to analyse the DOM release experiment were performed using OriginPro 9 (OriginLab), while the EEM data were analysed with MATLAB. All other analyses were performed using R version 3.6.1 for statistical computing (R Core Team, 2019).

From the EEMS results of the seasonal study three indicators were calculated: fluorescence index (FI), freshness index (FRESH), and humification index (HIX). The FI is used as an indicator of the source of DOM: high FI *c.* 1.8 indicates microbial and algal origin of DOM, while low FI *c.* 1.2 suggests terrestrial plant and soil derived DOM. The FRESH index is used as an estimator of how recently the DOM has been produced (*freshness*). Finally, HIX indicates the humification of DOM (i.e. amount of aromatic compounds) (Fellman, Hood, & Spencer, 2010). The relationships over time of CDOM and DOC with TSS, water depth, pH, conductivity, and the EEMS indexes were assessed on monthly averaged data using cross-correlation analyses (Zab-szék in 2017 was excluded from these analyses due to repeated complete droughts). Prior analyses the autocorrelation of the variables was removed by differencing the series with a lag of one. The successful removal of autocorrelation was confirmed by the Ljung–Box test.

3 | RESULTS

3.1 | Multisite comparison of the effect of groundwater and macrophytes

The characteristics and measured parameters of the 14 pans and corresponding groundwater wells analysed in the multi-site comparison are listed in Table 1 and Table S2. $CDOM_{pan}$ was almost always higher than the $CDOM_{groundwater}$ (paired *t*-test logCDOM: $t = 3.912$, $p = 0.002$; Figure 3a). Similarly, pH and conductivity were also usually higher in the pans than in the groundwater (paired *t*-test, pH: $t = 3.896$, $p = 0.002$, electrical conductivity: $t = 2.086$, $p = 0.057$). In the case of the soda pan that completely lacked macrophyte cover, the $CDOM_{pan}$ was very similar to $CDOM_{groundwater}$ well (Table 1: Unnamed pan). The comparison of individual parameters with $CDOM_{pan}$ detected no significant linear correlation (Table S3). However, the amount of non-groundwater related CDOM ($CDOM_{diff}$) showed significant correlation ($p < 0.05$) with *B. maritimus* cover as well as with the ratio of *B. maritimus* in the macrophyte cover (Figure 3c,d; Table S3). The *t*-test comparing the categories of the discrete parameters revealed that turbid pans had higher pH and TSS, and lower macrophyte cover than the coloured pans, while soda–saline type pans had higher groundwater pH and lesser *B. maritimus* cover than soda type pans (Table S5).

The backward selection of variables removed total emergent macrophyte cover and total area from model A, and chemical type from model B. According to AIC and subsequent Akaike weight calculation the reduced model B outperformed the reduced model A (Supplementary material and Table S6). The relative contribution of the variables to this model revealed that *B. maritimus* specific cover of the pans significantly explained 23.6% of the variation of $CDOM_{pan}$ ($p = 0.005$), while *P. australis* cover explained only 3.8% ($p = 0.009$; Figure 3b, Table S7). The second most important variable defining $CDOM_{pan}$ was $CDOM_{groundwater}$ followed by conductivity and optical type of the pans. Other variables in the model were all significant except $pH_{groundwater}$ but accounted for <8% of the variance each.

3.2 | Experimental release of DOM from macrophytes

At the end of the experiment, the plant material of *P. australis* lost 7.33 ± 0.15% (3.66 ± 0.075 g) dry mass, while *B. maritimus* lost 10.28 ± 2.79% (5.14 ± 1.40 g). The initial CDOM concentration in the experimental bottles was 39.23 ± 2.22 mg Pt/L and, by the end of the experiment, it increased in average to 1,190 and 3,900 mg Pt/L for *P. australis* and *B. maritimus*, respectively. The total CDOM release was 1,136 and 2,675 mg Pt/g dry weight loss for *P. australis* and *B. maritimus*, respectively. According to the Michaelis–Menten kinetics, at the end of the experiment CDOM concentration was 90.9 and 86.7% of the possible maximum (V_{max}) for *P. australis* and *B. maritimus*, respectively (Figure 4a).

The initial DOC concentration was 13.40 ± 0.099 mg/L and by the end of the experiment increased in average to 82 and 183 mg/L for *P. australis* and *B. maritimus*, respectively. The total DOC released was 78 and 125 mg/g dry weight loss for *P. australis* and *B. maritimus*, respectively. According to the Michaelis–Menten kinetics, at the end of the experiment the DOC concentration was 100.9 and 96.8% of the V_{max} for *P. australis* and *B. maritimus*, respectively (Figure 4b). The CDOM/DOC ratio increased linearly with significant parameters from 9 to 14.5 and from 16 to 21 for *P. australis* and *B. maritimus*, respectively (Figure 4c).

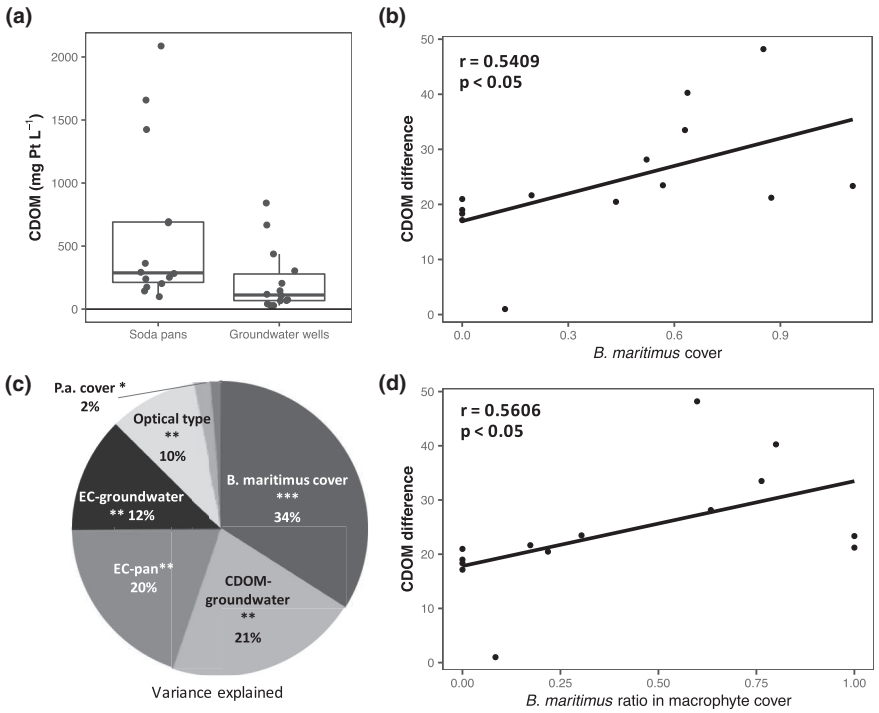


FIGURE 3 Multisite comparison of the factors related to coloured dissolved organic matter (CDOM) in 14 soda pans of the Carpathian Basin. (a) Comparison of CDOM concentration in soda pans and nearby groundwater; (b) variance of CDOM of the 14 pans explained by the different parameters based on linear model (reduced model A from Table S6). Significance of parameters according to ANOVA (Table S7) indicated by **: $p < 0.01$; *: $p < 0.05$. B.m. = *Bolboschoenus maritimus*, P.a. = *Phragmites australis*, EC = electrical conductivity. Correlation of the difference between CDOM concentration of soda pans and corresponding groundwater wells (square-root-transformed data) (c) with species-specific *B. maritimus* macrophyte cover; and (d) with the ratio of *B. maritimus* in the macrophyte cover

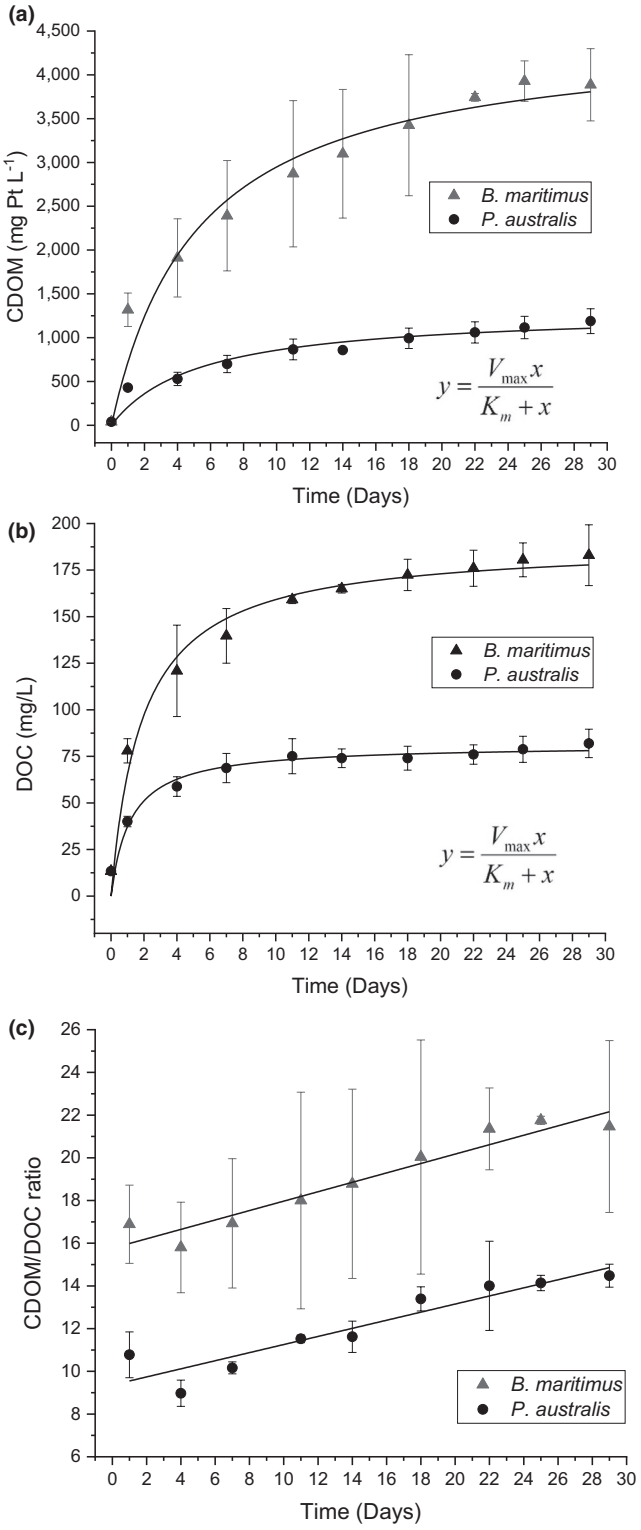


FIGURE 4 Experimental organic matter release from *Bolboschoenus maritimus* and *Phragmites australis* plant material. (a) Coloured dissolved organic matter (CDOM) release. Non-linear Michaelis–Menten kinetics-based curve fitting statistics for *B. maritimus*: $n = 28$; $df = 25$; $r^2 = 0.7881$; $V_{max} = 4495.6372$ $p \ll 0.0001$; $K_m = 5.2482$ $p = 0.0023$, and for *P. australis*: $n = 28$; $df = 26$; $r^2 = 0.8403$; $V_{max} = 1308.8554$ $p \ll 0.0001$; $K_m = 5.2816$ $p = 0.0002$. (b) Dissolved organic matter (DOC) release. Non-linear Michaelis–Menten kinetics-based curve fitting statistics for *B. maritimus*: $n = 28$; $df = 26$; $r^2 = 0.9197$; $V_{max} = 189.4330$ $p \ll 0.0001$; $K_m = 1.9014$ $p \ll 0.0001$, and for *P. australis*: $n = 28$; $df = 26$; $r^2 = 0.8596$; $V_{max} = 81.2560$ $p \ll 0.0001$; $K_m = 1.1827$ $p \ll 0.0001$. (c) Changes CDOM/DOC. Linear curve fitting statistics for *B. maritimus*: $n = 28$; $df = 26$; $r^2 = 0.5630$; intercept = 15.7668 $p \ll 0.0001$; slope = 0.2204 $p = 0.0028$ and for *P. australis*: $n = 28$; $df = 26$; $r^2 = 0.7529$; intercept = 9.3597 $p \ll 0.0001$; slope = 0.1896 $p \ll 0.0001$

3.3 | Seasonal comparison of a turbid and a coloured pan

The seasonal sampling was performed in 2 non-consecutive years (2014 and 2017) that had very different weather patterns. In 2014 temperature was >1.5°C higher than the historic mean (i.e. monthly average measured between 1981–2010), whereas precipitation in the preceding period (second half of 2013) was only 75% of the historic mean, while in the second half of 2014 it was 155% of usual. Meanwhile, in 2017 both temperature and precipitation were close to normal (Figure S1).

As expected by the definition (Boros et al., 2013) and in accordance with the multi-site analysis, the turbid Zab-szék had substantially higher turbidity than the coloured Sósér pan throughout most of the study period (Table 2, Figure 5a). Also, in accordance with the multi-site analysis, throughout the 2 years, the pans differed in respect of pH but not conductivity (Table 2, Figure 5c,d). Water depth showed high variation in both pans (Figure 5b), although Sósér was slightly deeper than Zab-szék (Table 2). Water depth changes indicated that the hydrology of the 2 studied years followed different patterns as for both pans the beginning of the year in 2014 was characterised by low water depth, which increased from September–October until the end of the year. Meanwhile, in 2017 both pans had higher water levels at the beginning of the year until August, when the water levels decreased and remained low until the end of the study period (Figure 5b). Both CDOM and DOC were higher in Sósér than in Zab-szék (Table 2, Figure 5e,f). The concentration of CDOM and DOC also differed between the 2 years with higher values for both pans in 2014 than in 2017 (Table 2, Figure 5e,f). More precisely, the highest CDOM and DOC levels were all measured in Sósér in 2014 between January and August, which corresponded to the lowest water level period of the given year (Figure 5b). In this period, the mean concentration of CDOM was 6,649 mg Pt/L and DOC was 563 mg/L, while for the rest of the year was 1,294 mg Pt/L and 111 mg/L for CDOM and DOC, respectively.

The two pans also differed in respect of the indicators calculated from the EEMS (Figure 6). Sósér had higher HIX, while Zab-szék had FRESH (Table 2, Figure 6b,c). In addition, both pans had generally higher FRESH values in summer and Zab-szék had a prominent FRESH peak in the beginning of summer (29 May; Figure 6b). The FI did not differ between the two pans (Table 2), although it showed much higher variation in Zab-szék with prominent peaks in summer and autumn (Figure 6a). For both pans, the mean FI index was close

TABLE 2 Mean and standard deviation of the measured parameters of the turbid and coloured soda pan in the 2 years of seasonal monitoring

	Sósér				Zab-szék			
	2014		2017		2014		2017	
Parameter	Mean	*SD*	Mean	*SD*	Mean	*SD*	Mean	*SD*
TSS	180.8	293.0	68.7	71.1	2325.9	2201.9	2100.9	1618.3
Depth	18.6	15.3	26.8	14.3	13.1	12.1	11.3	9.6
pH	9.26	0.54	9.23	0.40	9.60	0.28	9.61	0.21
EC	5.72	3.45	6.49	3.79	5.64	3.66	7.05	6.68
CDOM	5888.7	2908.6	1628.2	508.7	470.4	200.8	279.1	127.3
DOC	437.3	268.5	214.6	108.4	69.1	48.0	49.4	10.8
FI	–	–	1.228	0.028	–	–	1.234	0.049
FRESH	–	–	0.608	0.030	–	–	0.736	0.091
HIX	–	–	17.47	1.689	–	–	7.143	1.436

CDOM, coloured dissolved organic matter; DOC, dissolved organic carbon; EC, electrical conductivity; FI, fluoresence index; FRESH, freshness index; HIX, humification index; TSS, total suspended solids.

to the value expected for DOM of terrestrial and soil origin (Sósér: FI_{median} = 1.235; Zab-szék: FI_{median} = 1.236).

The cross-correlation analyses revealed that in most of the cases both CDOM and DOC showed the strongest significant correlations with parameters measured at the same time (lag = 0; Table S8). The only exceptions were the correlation of DOC in Zab-szék in 2014 with TSS (strongest correlation at lag = 2), depth and pH (lag = −5), and DOC in Sósér in 2017 with HIX (lag = −3) Therefore, here we focus only on the presentation of lag = 0 correlations (Table 3). In the case of Sósér, DOC concentration was significantly and positively correlated with TSS, pH, conductivity, and FRESH index, and negatively with depth. Meanwhile, in Zab-szék DOC showed significant (positive) correlation only with depth and conductivity (Table 3). The CDOM concentration significantly correlated with mean depth, pH, and conductivity in almost all cases , apart from pH in Sósér in 2017 and conductivity in Zab-szék in 2014. Interestingly, the sign of the correlations with CDOM depended on the pan: in Sósér CDOM positively correlated with pH and conductivity, and negatively with depth, while in Zab-szék CDOM negatively correlated with pH and conductivity, and positively with depth.

4 | DISCUSSION

The results of our study indicate—as we hypothesised—that the CDOM variation in the soda pans of the Carpathian basin is highly influenced by groundwater and emergent macrophyte cover but—contrary to our hypothesis—it is not driven by the extent of the overall macrophyte cover. Furthermore, we demonstrated that the variation of DOC and CDOM concentrations of these pans is related to the variations in pH, conductivity, and water depths, and it is presumably influenced by yearly variations in hydroperiods and intrinsic pan properties such as turbidity.

4.1 | Groundwater as allochthonous source of CDOM

Plant-derived CDOM in inland waters originates either from macrophytes or from terrestrial vegetation of the catchment via surface or groundwater inflow (i.e. allochthonous source) (Einarsdottir et al., 2017; Lapierre & Frenette, 2009; V.-Balogh, Presing, Hiripi, & Vörös, 1998; Wetzel, 2001). As no watercourse enters the pans studied here, the role of surface inflow in their water budget is negligible (Boros et al., 2013), and therefore CDOM content is expected to be primarily derived from macrophytes and groundwater inflow. The multi-site comparison demonstrated that the CDOM concentration of the pans is related to the CDOM concentration of groundwater. Groundwaters store and release carbon to surface waters in amounts that are meaningful for global budgets (Downing & Striegl, 2018) and import of terrestrial carbon into lakes via groundwater seepage can be substantial even in lakes with hydrology dominated by surface water inflow (Einarsdottir et al., 2017). In areas of lower relief, shallow basins can be the focus of local discharge and evaporation from regionally extensive groundwater systems (Deocampo & Jones, 2014) and modern continental evaporates such as endorheic soda lakes and pans typically accumulate within groundwater discharge (Warren, 2006). The importance of such groundwater driven processes was also identified behind the formation and hydrology of soda pans of the Danube–Tisza Interfluve (Mádl-Szőnyi & Tóth, 2009; Simon et al., 2011). The groundwaters analysed here had relatively high pH (median: 8.60, range: 7.02–9.56), which—considering the pH-dependent dissolution of humic substances (Aiken et al., 1985)—probably contributed to their high CDOM content. Considering the hydrological importance of groundwater, it is not surprising that the high groundwater CDOM explained a substantial part of the variation of the CDOM concentration of the soda pans. Furthermore, the mean FI indexes measured by EEMS in the seasonal monitoring were close to 1.2, which is considered to indicate

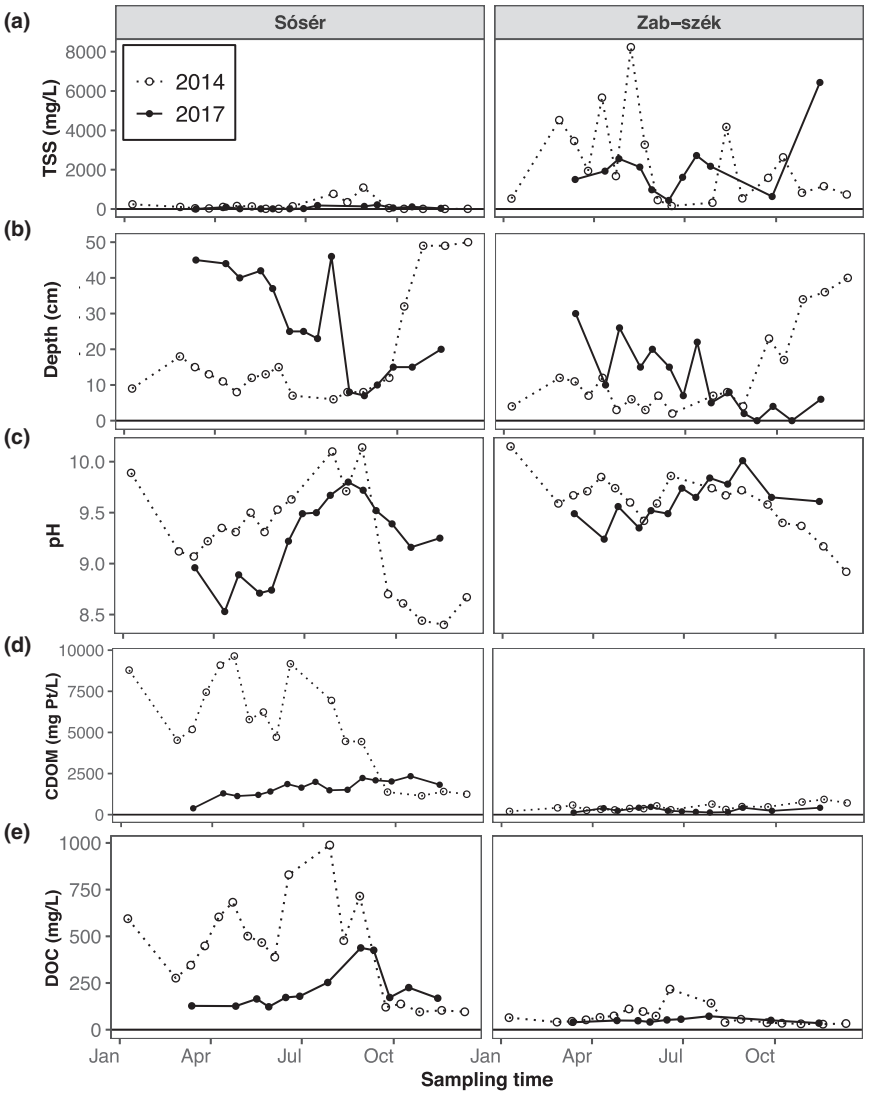


FIGURE 5 Multiyear comparison of the temporal changes of environmental parameters in Sósér (Sos) and Zab-szék (Zab) soda pans in 2014 and 2017. (a) Total suspended solids (TSS); (b) mean water depth; (c) pH; (d) electrical conductivity (EC); (e) coloured dissolved organic matter (CDOM); (f) dissolved organic carbon (DOC)

plant- and soil-derived organic matter (Fellman et al., 2010), further enforcing the partly terrestrial origin of the DOM of the pans.

4.2 | Autochthonous emergent macrophyte cover type influences CDOM content

The CDOM content of the pans also depended on the species-specific emergent macrophyte cover, with higher *B. maritimus* ratio pans having higher CDOM content than those dominated by *P. australis*. While in the case of lakes, macrophyte-derived DOC is considered to contribute only to 1–20% of the total DOC, for wetlands and small lakes the role of macrophytes in the carbon budget can be substantial (Reitsema, Meire, & Schoelynck, 2018; Sobek, Söderbäck, Karlsson, Andersson, & Brunberg, 2006). However, in our linear models, the CDOM content variance of the pans was not explained by the overall emergent macrophyte cover, while *B. maritimus* species-specific cover was the most important factor (23% of variance explained).

The importance of *B. maritimus* specific cover was corroborated by the results of the DOM release experiment, which also showed that more than triple CDOM and more than double DOC are released from *B. maritimus* than from *P. australis*. While DOM release from *P. australis* has been studied before, to the best of our knowledge this is the first report for *B. maritimus*. The DOC release results for *P. australis* presented here (82 mg/L) compare well to those from a previous experiment conducted under similar conditions (75 mg/L) (V.-Balogh et al., 2006), indicating high reproducibility of our experiment. *P. australis* also released less DOC when compared to other emergent macrophytes, such as crofton weed (*Eupatorium adenophorum*), water oats (*Zizania latifolia*), oriental pepper (*Polygonum orientale*) (Qu et al., 2013), or seepweed (*Suaeda salsa*) (Qi, Xue, & Wang, 2017). All this indicates that common reed (*P. australis*) is a relatively low DOC-releasing emergent macrophyte and accordingly, it is essential to consider the composition of emergent macrophytes when assessing macrophyte impact on the carbon balance of aquatic systems.

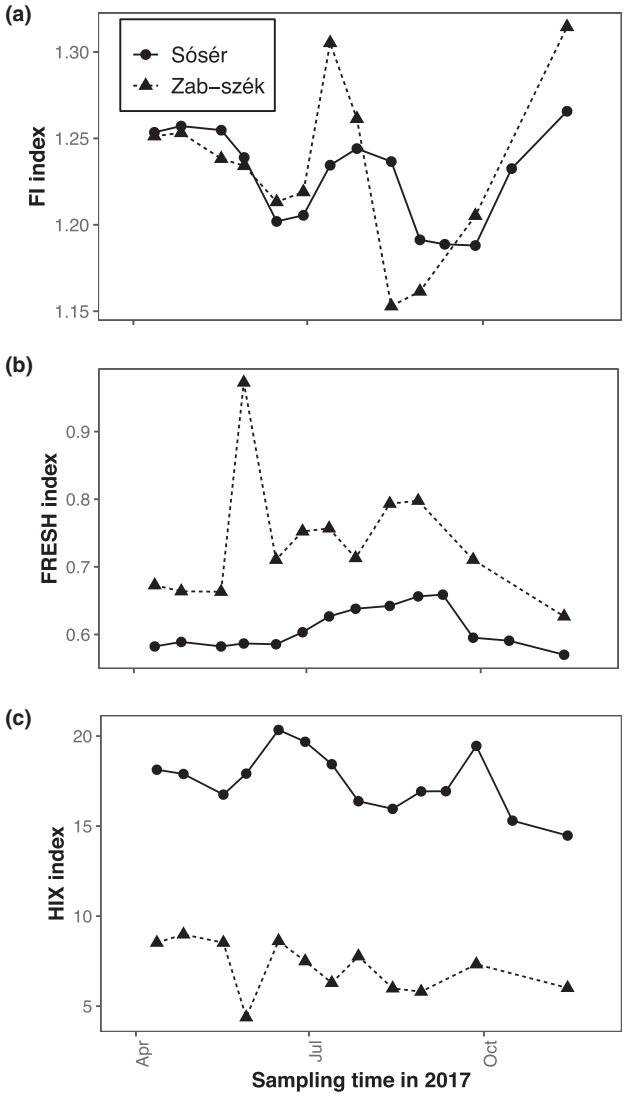


FIGURE 6 Temporal changes of dissolved organic matter (DOM) characterising indices derived from fluorescence excitation emission matrix spectroscopy (EEMS) in Sósér and Zab-szék soda pans in 2017. (a) Fluorescence index (FI) indicating the source of DOM with high values (FI ≈ 1.8) suggesting DOM derived from extracellular release and leachate from bacteria and algae, and low values (FI ≈ 1.2) indicating plant and soil derived organic matter. (b) Freshness index (FRESH) indicating contribution of recently produced DOM. (c) Humification index (HIX) indicating humic substance content or extent of humification of DOM (Fellman et al., 2010)

The overall DOC release during the experiment reached values close to the maximum expected for both species, while CDOM release did not reach the expected maximum for either species. This contrasting dynamic between CDOM and DOC resulted in continuously increasing CDOM/DOC ratio. To better mimic natural conditions, our experiment was not conducted under sterile conditions. Therefore, the increase in the ratio of CDOM suggests aerobic microbial degradation of the labile carbon fraction and concomitant accumulation of recalcitrant CDOM. The importance of microbial degradation in the consumption of released DOC was also demonstrated by the experiment of Qi et al. (2017) were the amount of DOC released from *P. australis* was nine times higher under sterile conditions than without inhibition of microbial degradation.

Furthermore, we have to emphasise that the pH of the water used in the experiment was lower (pH 8.40) than the pH of almost all pans analysed in the multi-site comparison (mean pH 9.36). In a decomposition experiment, increasing pH has been shown to correlate with increasing dry mass loss from macrophyte litter (Krachler, Krachler, Stojanovic, Wielander, & Herzig, 2010), which, together with the pH-dependent dissolution of humic substances, suggests even higher release of DOC and CDOM from macrophytes in the pans than in our experiment. However, the CDOM/DOC ratio at the end of the experiment was 14 times higher for *P. australis* and 21 times for *B. maritimus* than the average ratio of 6.6 measured for 84 soda pans of the region (Boros et al., 2017). Probably, in natural habitats CDOM is also degraded by photochemical reactions, which are considered as a significant contributor to organic carbon mineralisation in shallow high DOC lakes (Koehler, Landelius, Weyhenmeyer, Machida, & Tranvik, 2014). In summary, it is likely that the autochthonous plant-derived DOM of soda pans depends on the species composition of the emergent macrophytes and the interplay of microbial and photochemical degradation.

4.3 | Potential drivers of the seasonal variation of CDOM and DOC

The two soda pans studied in the seasonal comparison differ in respect of species-specific emergent macrophyte cover (57% *B. maritimus* cover in Sósér and 1% in Zab-szék, and *P. australis* cover 38 and 16%, respectively) and in their optical characteristics (i.e. coloured Sósér and turbid Zab-szék), which might affect photochemical reactions. Although both pans had very high CDOM and DOC concentration, in the case of the coloured pan these concentrations were extremely high. The multi-site comparison and DOC release experiment suggests that the extensive *B. maritimus* macrophyte cover of Sósér contributed to its extreme CDOM and DOC concentrations. Meanwhile, Zab-szék compared to Sósér had slightly higher pH, lower water depth, and consequently intermittent hydrology with several droughts in 2017. The two pans also differed in DOM quality (i.e. EEMS) as Sósér had high HIX, suggesting high ratio of plant-derived recalcitrant DOM, while Zab-szék had high FRESH, indicating high ratio of freshly produced autochthonous DOM.

In addition, substantial differences in the hydrology and overall CDOM and DOC concentrations of the 2 years monitored were also observed, which were probably related to the differences in temperature and precipitation regimes of the study years and the preceding periods. Specifically, considering the importance of groundwater in the hydrology of the soda pans in this region (Mádl-Szőnyi & Tóth, 2009), the combination of decreased precipitation followed by high temperature in 2013 and 2014 might have caused increased evapotranspiration from soils, leading to decreased

TABLE 3 Results of cross-correlation at lag = 0 of coloured dissolved organic matter (CDOM) and dissolved organic carbon (DOC) and environmental parameters of the turbid and coloured soda pans. Significant correlations ($p < 0.05$) are in bold

	CDOM			DOC		
	Sósér		Zab-szék[a]	Sósér		Zab-szék[a]
	2014	2017	2014	2014	2017	2014
TSS	0.316	0.598	0.355	**0.737**	**0.745**	0.122
Depth	**−0.750**	**−0.829**	**0.809**	**−0.758**	**−0.778**	**0.622**
pH	**0.778**	0.563	**−0.792**	**0.930**	**0.839**	0.414
EC	**0.802**	**0.660**	−0.447	**0.994**	**0.870**	**0.951**
FI		−0.297			−0.568	
FRESH		0.181			**0.809**	
HIX		−0.225			−0.125	

[a]Measurements from 2017 for Zab-szék were omitted from these analyses because of missing data due to drought of the pan.

groundwater levels, and consequently less groundwater influx to the pans. This can explain the lower water levels measured for both pans in the beginning of 2014 compared to those measured during the cooler and less dry beginning of 2017. Similarly, the opposite water level trends in autumn (i.e. increase in 2014 and decrease in 2017) could be explained with the unusually high precipitations in the second half of 2014.

In Sósér the lower water level period of 2014 coincided with the highest DOC and CDOM concentrations measured. In this period, the mean DOC concentration of the pan was 563 mg/L, which is more than an order of magnitude higher than the average of wetlands and remarkable even among soda lakes and pans (e.g. Boros et al., 2017; Butturini, Herzsprung, & Lechtenfeld, 2020; Jirsa et al., 2013). Both the CDOM and DOC concentrations of Sósér were negatively correlated with water depth throughout the study period, which suggests evaporation driven concentration. This is supported by the positive correlation of CDOM and DOC to conductivity and pH as both are also expected to increase with decreasing water levels due to concentration of inorganic ions. Furthermore, considering the pH dependence of the dry matter loss from macrophyte litter (Krachler et al., 2010), the higher pH of the period could have further aggravated the OM release from the dense *B. maritimus* dominated macrophyte cover of Sósér. Turbidity positively correlated with DOC, suggesting that in this otherwise low turbidity pan, organic carbon defines turbidity opposite to clay minerals in turbid pans (Boros et al., 2013).

By contrast, in the turbid Zab-szék correlation between depth and both CDOM and DOC was positive suggesting that possibly groundwater itself was the primary allochthonous source of CDOM and DOC. The results of the multi-site comparison also corroborate this as for this pan—exceptionally among the other studied pans—CDOM content of the nearby groundwater well was almost double of the CDOM content of the pan. Interestingly, CDOM and DOC correlated differently with pH and conductivity. For CDOM, the correlations were negative, which, considering the lower pH and conductivity of the nearby groundwater well, supports the groundwater origin theory of $CDOM_{pan}$. Meanwhile, for DOC, the correlations were positive, which is seemingly contradictory to this theory. As DOC measures both labile and recalcitrant organic carbon, while CDOM reflects more recalcitrant organic carbon, a potential explanation to the increasing DOC content at higher conductivity could be inhibition of biodegradation of labile DOM by salinity, which is a strong microbial inhibitor (Székely et al. 2013). However, it is also possible that higher DOC but lower CDOM concentrations at high conductivity reflect non-humic freshly produced autochthonous DOM, which together with the lesser *P. phragmites* dominated macrophyte coverage, suggests the influence of phytoplankton and microbial communities on the DOM. This explanation is enforced by the contrasting microbial community of the two pans (Szabó et al., 2017) and by the peaks of FI index in Zab-szék, which are potential indicators of phytoplankton and microbial blooms suggesting greater importance of non-macrophyte related autochthonous carbon dynamics in Zab-szék compared to Sósér.

In a broader perspective, our results demonstrate that in endorheic water bodies—particularly those lacking surface inflow—groundwater can be an important source of organic carbon that should be accounted for in carbon budget calculations. We also showed that emergent macrophytes are essential sources of recalcitrant organic carbon. Although when estimating macrophyte effect, species composition has to be also considered since common reed (*P. australis*), one of the most common emergent macrophytes on a global scale has relatively low organic carbon release compared to other species such as the cosmopolitan bulrush (*B. maritimus*), for which this study comprises the first report of experimental decomposition measurements. Finally, we demonstrated that the record high DOC values (0.5–1 g/L) measured in the soda pans of the Carpathian basin are the result of the interplay of intrinsic soda pan characteristics such as *B. maritimus*-dominated macrophyte cover and most importantly persistent low water levels that occur in consequence of weather anomalies. More precisely, we showed that high organic carbon content periods follow extreme warm and dry seasons. Considering that such weather patterns might increase in frequency in the near future due to the ongoing climate change, soda pans could become increasingly important hotspots of

terrestrial carbon processing, urging further studies exploring the carbon biogeochemistry of soda lakes.

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CONFLICT OF INTEREST

We declare that there is no actual or potential conflict of interest.

DATA AVAILABILITY STATEMENT

The seasonal monitoring data and fluorescence spectra used for the EEMS analyses are available on the online repository at http://urn.kb.se/resolve?urn=urn:nbn:se:uu:diva-385197.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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