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Extreme guanotrophication by phosphorus in contradiction with the productivity of alkaline soda pan ecosystems

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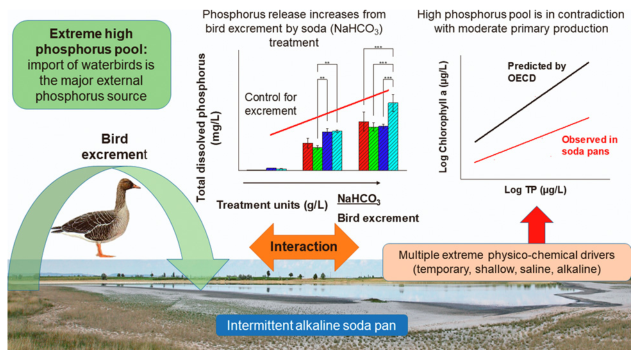
HIGHLIGHTS

- Waterbirds can cause extreme guanotrophication (max. 2500 mg $P/m^2/y$) in waters.
- Alkaline soda pans (pH > 9) have characteristic physico-chemical properties.
- Excrement of waterbirds is the major phosphorus source (>50%) of soda pans.
- Physico-chemical factors interact with P loading (mean: 185 mg $P/m^2/y$) of waterbirds.
- Extremely high P pool (mean: 5.17 mg/L) coupled with moderate primary production

GRAPHICAL ABSTRACT



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ABSTRACT

Waterbirds as nutrient vectors can cause high phosphorus loading in shallow inland aquatic ecosystems. The main goal of this study was to determine the causal relationships between the characteristic physico-chemical properties of intermittent (temporary) alkaline soda pan (playa) ecosystems and specific (surface and volume-related) P loading of waterbirds by in situ field investigation, estimation as well as laboratory experiments using standard methods. In addition, our aim was to estimate the contribution of groundwater and precipitation to the total phosphorus pool of soda pans in Hungary.

The estimated high specific external P loading of waterbirds (mean: 185 mg $P/m^2/y$, 3.32 mg P/L/year) can explain the majority of the hypertrophic TP pool (mean: 5.17 mg/L, 64%) in soda pans, which is mediated by large-bodied herbivorous (e.g. geese and ducks) and medium-bodied omnivorous (e.g. gulls) waterbirds, who are important external nutrient importers and major phosphorus source. The results also confirm the hypothesis that groundwater (3%) and precipitation (5%) together account for a smaller estimated (8% in this study) contribution to the hypertrophic TP pool in soda pans, while the contribution of waterbirds (64% in this study) to the TP is much higher (64–100%). In this study, the remaining part of TP (maximum 28%) pool can be explained by internal P sources.

Soda pans are characterized by physical and chemical characteristics coupled with high densities of waterbirds, as biotic mediators of external P sources, which together cause the maintenance of high concentrations of P-forms. The extreme guanotrophication by high P loading of herbivorous waterbirds causing a hypertrophic state is in contradiction with the limited primary production of natural soda pans. This unique phenomenon can be explained by the multiple impact of prevailing extreme physico-chemical drivers (intermittent hydrological cycle, shallow water depth, high turbidity, salinity, alkalinity) and by the specific nutrient cycle of these alkaline soda ecosystems.

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1. Introduction

Waterbirds can have a significant impact on biochemical cycles, energy flow and production in aquatic ecosystems and several supporting or regulatory ecosystem services (Green and Elmberg, 2013). The term "Guano" applies to natural mineral deposits consisting of excrements, eggshells sand carcasses of dead birds, especially by seabirds (Schnug et al., 2018), but guanotrophication is a popular term for the nutrient enrichment of inland waters by waterbird excrements and not only in the case of seabirds (Leentvaar, 1967). Sometimes their high population density and active metabolism can lead to eutrophication, especially through excessive phosphorus (P) loading in inland waters (Adhurya et al., 2018).

Extremely high TP concentration (14 mg/L) was observed in the natural Fehér-Lake soda pan (Hungary), with the highest record of surface-related P loading (2500 mg P/m^2/year) in the world due to guanotrophication (Boros et al., 2008a), and most of the Hungarian soda pans belong to the upper range of TP and surface/volume-related P loadings by waterbirds. Although the P-loading of waterbirds varies greatly among Hungarian soda pans and also over time (Boros et al., 2008a, 2016), and most of them have high waterbird density and/or diversity above the average of waterbird assemblages in the inland waters of the region (Faragó, 2016), due to their favourable conditions for waterbirds (Boros et al., 2013).

The soda pans in the Carpathian Basin are located on the border of the East-Atlantic and the Black Sea-Mediterranean flyways, thus the region is a very important continental non-resident breeding and stopover site for African–West-Eurasian continental migratory waterbirds (BirdLife, 2010). Guanotrophication can affect production-decomposition processes through various trophic relationships. The net nutrient and energy import guild, which is largely made up of large herbivorous waterbird species (e.g., geese and ducks) provides the majority (>60%) of avian nutrient P loading into these aquatic ecosystems, effectively contributing to hypertrophic conditions (Boros et al., 2008a, 2008b, 2016), which often leads to net heterotrophy (Vörös et al., 2008), as waterbirds can influence both primary and heterotroph productions (Batanero et al., 2017). In addition, the lowest production and respiration rate (Pro/Res) and the extremely high dissolved organic carbon concentration (polyhumic) in several soda pans can be explained by plant-derived organic matter of both autochthonous macrophytes and allochthonous terrestrial vegetation of the watershed through groundwater inflow in the Central European region (Boros et al., 2020).

Since soda-lake formation depends on low levels of dissolved calcium and magnesium, as well as on the dominance of carbonates, they represent the most stable permanent high-pH environment (pH > 9) on Earth, which clearly distinguishes them from other inland saline waters. Most of them are shallow, with several extreme physical and chemical conditions, special biogeochemical cycle and unique ecosystems (Boros et al., 2017; Boros and Kolpakova, 2018). Soda lakes and pans (playas), particularly in tropical regions, are regarded as the most productive environments in the world, with primary producers having unlimited access to CO_2 in the form of dissolved carbonates (Grant, 2004; Duckworth et al., 1996). Furthermore, soda lakes are fertile habitats for an enormous diversity of alkaliphilic viruses and microbiotas (Grant and Jones, 2016), which are able to cope with the multiple extreme conditions that prevail in these ecosystems (Szabó et al., 2017). High biomass of decomposers and phytoplankton in turn supports abundant consumers, including brine shrimps, crustacean zooplankton, insects, fishes (only in permanent lakes) and waterbirds (Horváth et al., 2013; Boros et al.,2006a,b, 2008a,b, 2013; Kingsford et al., 2020).

Considering climate change trends common in most endorheic arid regions (i.e., increased temperature and modified precipitation regimes), extremely high dissolved 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 macrophyte cover and substantial groundwater inflow might become organic carbon processing hotspots (Boros et al., 2020). Phosphate is a key chemical component of biomolecules (e.g. nucleotids, adenosine triphosphate), and it is generally limited to micromolar levels in the environment, except for modern carbonate-rich lakes - like endorheic soda lakes and pans - which can accumulate dissolved phosphate because calcium is sequestered into carbonate minerals (Toner and Catling, 2020). The nitrogen and phosphorus ratio is often extremely low in these waters ($N/P < 1$), because high temperatures and alkalinity promote NH_3 emanation losses from soda lakes, thus there is no correlation between nitrogen (N) loading by waterbirds and N concentration in the water (Boros et al., 2008a, 2016; Clarisse et al., 2019).

The main objective of this study was to determine the causal relationships between the characteristic physico-chemical properties (water depth, salinity, $NaHCO_3$, pH) of intermittent (temporary) soda pans and the specific (surface and volume-related) P loading of waterbirds based on in situ field estimation and ex situ laboratory experiment. We hypothesize that the extremely large pool of P-forms in the water is due to the interaction of characteristic physico-chemical properties and P loading of waterbirds. The second aim of the study was to evaluate the relationship between seasonal variation of P loading by waterbirds and P-forms in soda pans. For this purpose, we hypothesize that there is an indirect delayed relationship between the P loading by waterbirds and P pools in the water. The third objective was to estimate the contribution of groundwater and precipitation to the annual average TP pool in the soda pans. For this, we hypothesize that they have together a non-dominant (<50%) contribution to TP compounds in the soda pans compared to waterbirds. Expected outcomes of the results can significantly contribute to the knowledge of the source and biogeochemical cycle of P in endorheic soda aquatic ecosystems, which attributes can be increased by climate change trend as they are alkaline hotspots of dissolved carbon and P in the world.

2. Methods

2.1. Study sites

Soda lakes and pans are formed in closed endorheic basins (i.e., limited drainage basins), where evaporation exceeds water outflow, the level of calcium (Ca^{2+}) and magnesium (Mg^{2+}) is low, while sodium (Na^+) and carbonates ($HCO_3^- + CO_3^{2-}$) are dominant (>25e%) ions (Boros and Kolpakova, 2018). The studied soda pans are very shallow (mean depth < 0.5 m) endorheic polymictic waters, and they are located in the central area of the Carpathian Basin (Central Europe), on the interfluve area of the Danube and Tisza rivers (Fig. 1). Among the selected soda pans, Böddi-szék has Na–Cl > HCO_3, while Kelemen- and Zab-szék have Na–HCO_3–Cl dominant ion composition (Boros et al., 2014). These chemical compositions are among the most characteristic chemical types of soda and soda-saline inland waters in Eurasia (Boros and Kolpakova, 2018).

The climatic conditions of the region (i.e., continental under the influence of both oceanic and Mediterranean climates) together with the shallowness of the soda pans lead to high water level and temperature fluctuations. Changes in water levels are particularly important because they often result in intermittent hydroperiods and affect the concentration of both organic and inorganic compounds, and there are no inlets and outlets in these endorheic systems. (Boros et al., 2013, 2017).

The primary source of the high Na–HCO_3–Cl— content of soda pans in the regional discharges from upwelling deep saline groundwater, enhanced by evaporation and groundwater inflow, which typically exceeds the surface-related watershed inflow and precipitation (Simon et al., 2011), while surface related watershed is negligible as usually no significant watercourse enters these aquatic systems (Boros et al., 2013).

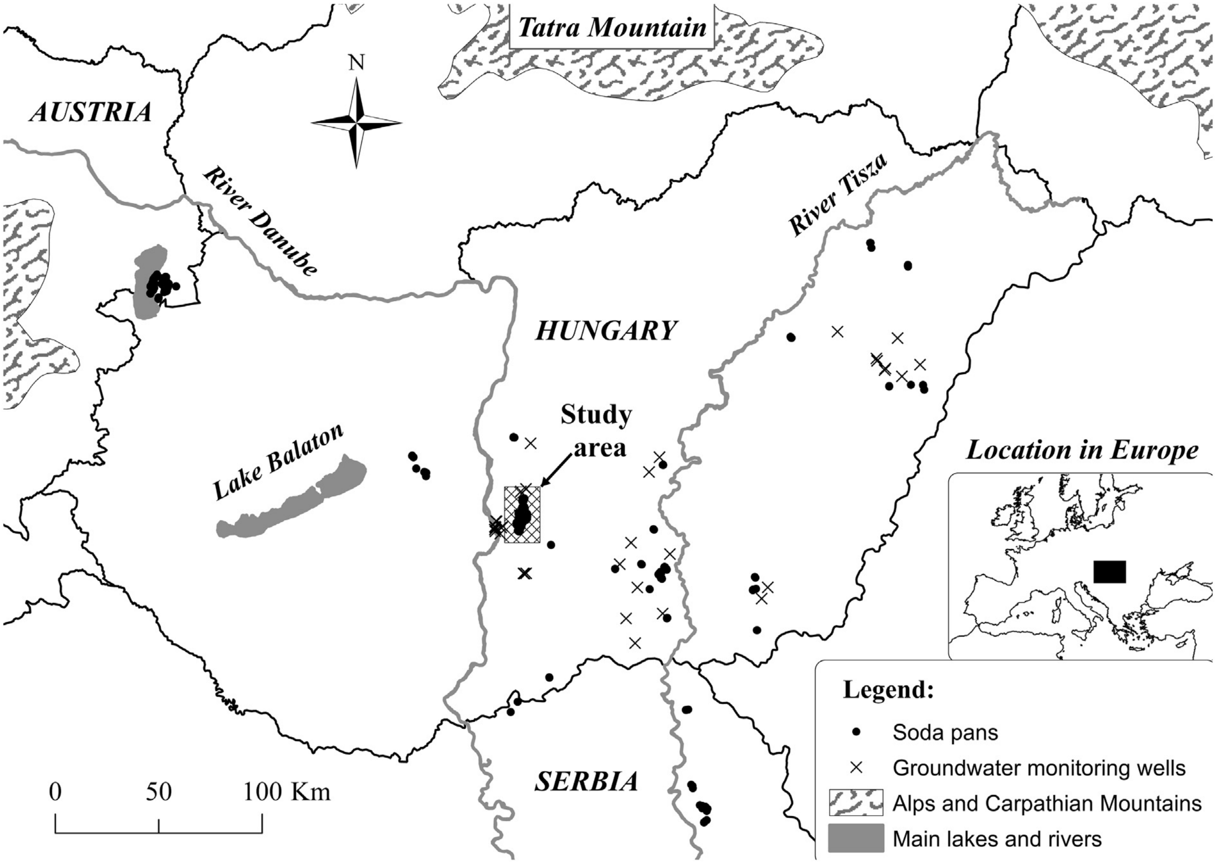

Fig. 1. Location of the study area with soda pans and selected representative groundwater monitoring wells in the Carpathian Basin (location of all the soda pans in the region based on Boros et al., 2017) Böddi-szék pan: N: 46.7666; E: 19.1500 Kelemen-szék pan: N: 46.7973; E: 19.1743 Zab-szék pan: N: 46.8342; E: 19.1748.

Based on optical characteristics these soda pans are categorized into two groups: turbid pans with inorganic suspended solids (ISS) as the main source of turbidity (i.e., contribution of ISS to light attenuation (Kd) exceeds 50%), and the coloured (brown) pans, where the contribution of coloured dissolved organic matter dominates Kd (>50%). Submerged and floating macrophytes are sparse or absent from the open water areas of both turbid and coloured pans. The common marshland vegetation (Bolboschoeno-Phragmitetum) on the shoreline is characterized primarily by a variable proportion of emergent macrophyte species, *Bolboschoenus maritimus* and *Phragmites australis*. The investigated pans have international importance for waterbird assemblages (regularly >20,000 ind.) and are unique wetland type under the Ramsar Convention (Boros et al., 2013).

2.2. Estimation of the P loading of waterbirds

The P-loading of waterbirds was estimated by determining the abundance of waterbird populations and the nutrient content of their excrement, according to Boros et al. (2008a, 2016). Waterbirds in the open water of the soda pans were counted with binoculars (8×42 and 10×42) and spotting scopes (zoom 20–60 $\times$ 78) in daylight, at 14-day intervals (biweekly) throughout 2017. At the same time, water sampling was carried out in three soda pans as repetitions (Böddi-szék, Kelemen-szék, Zab-szék). Daily waterbird abundance (individuals/m^2) was calculated from the mean of the biweekly counts for each month. The contribution of waterbird populations to the daily nutrient loading was estimated by using daily net rates data of P excretion, which are listed in Table S1. We used a linear time defecation rate assumption in our estimation. Each daily total P excretion data (g/day/individual) was modified by a species-residency time correction factor (RTF: residence time in hours on the soda pans during 24 h) on the water surface based on observed diurnal and nocturnal activity. Daily net P excrement data and waterbird species RTFs are listed in Table S1. The biweekly total loading of waterbirds $= \Sigma$ species ($A \times E \times RTF \times D$), where A (ind./m^2) is the daily mean of abundance of waterbird species for each month, E (g/day/ind.) is the daily net rate of P in the excrement of each species, RTF is the daily residency time factor (RTF: hours spent on soda pans/24 h) of each species on the open water and D (n days) is the number of days of each month. The annual cumulative net P loading was determined by summing the two-week mean loadings. Surface-related data (mg P/m^2/year) was calculated as the sum of loading quantities, measured every two weeks divided by the actual size of the open water each month. The volume-related unit (mg P/L/year) was calculated based on the sum of surface-related data (mg P/m^2/year) and yearly average of water depth (m).

2.3. Water sampling and measurements

During the growing season from 12 of April to 14 of November in 2017 water samples were taken from the open water surface at 14-day intervals (every two weeks) from the soda pans (Böddi-szék, Kelemen-szék, Zab-szék) with three repetitions of each sampling.

Very shallow (average depth < 0.5 m) polymictic turbid soda pans have relatively uniform flat bottom, with only small differences in elevation except for the shoreline. Therefore, for each sampling, water depth, conductivity and pH were measured at a single open water location at a sufficient distance from the shoreline with water depth (range: 0.02–0.26 m) representative of the pan using a centimeter-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 in plastic bottles and were transported to the lab, where filtered and nonfiltered samples were stored frozen until they were measured within a few weeks. Salinity was calculated from conductivity using the following formula (Boros et al., 2014):

$$\text{salinity (mg/L)} = 0.8 \times \text{Conductivity } (\mu S/cm) \tag{1}$$

The TP concentration was measured spectrophotometrically after potassium-persulfate digestion from unfiltered water samples (Menzel and Corwin, 1965), while the total dissolved phosphorus (TDP) was quantified from filtered samples (Whatman RC 55, 0.45 μm pore size) with the same method as for TP. The concentration of soluble reactive phosphorus (SRP) was determined from filtrates based on the method of Murphy and Riley (1962). The same methods were used for all P measurements as responsible variables in the ex situ laboratory experiment. All chemicals used in the measurements were of analytical grade. For laboratory investigations the ultra-pure water (18 MΩ cm^{-1}) was produced by applying a WasserLab Autwomatic unit (Labsystem Ltd., Budapest, Hungary).

2.4. Experiment on release of P from goose excrement

As Greylag Goose (*Anser anser*) is one of the most important net P importer species in this ecosystem (Boros et al., 2008a), its fresh excrement (approximately 70 pieces) was collected from the field for laboratory measurements and experiments. The pieces of excrement were lyophylized at −57 °C in an Alpha 1 (Christ) equipment (at 200 Pa for 72 h) thereafter shredded and mixed (finally sum 50 g dry mass).

According to the first goal of this study, the P loading of waterbirds was represented by Greylag Goose excrement as the first factor in the ex situ laboratory experiment by 0 (control), 1 and 2 g/L doses as a real volume of P loading of waterbird population in the soda pans. The soda alkaline chemical effect was applied by sodium bicarbonate ($NaHCO_3$) as second factor in the same salinity gradient than it prevails in the soda pans as: 0 (control) 2.5, 5, 7.5, 10 g/L concentration. The excrement was extracted and $NaHCO_3$ dissolved by one litre ultrapure water (Milli-Q) for each bottle of experimental units. All combinations of the two involved factors as experimental treatment units were separated in Latin-square arrangement with three repetitions of each unit respectively. The key response variables were the same three P-forms (TP, TDP, SRP) pH and salinity were measured in the experiment, which also were parallel measured in the soda pans. The bottles of treatment units including the controls were kept under aerobic conditions resemble on atmospheric air by aeration pump throughout the experiment. The incubation was performed in three replicates at room temperature (21 °C) for 24 h, because the result of the applied pre-experiment showed that TP release reached the peak during one day under our laboratory circumstances, as a simplified system on standard temperature (21 °C) without complex biogeochemical cycle. The response P variables were measured one times at the end of experiment with the same method as in the soda pans.

2.5. Other external P loading

Groundwater is the most important water source of the investigated soda pans (Simon et al., 2011), and direct water inflow on the surface is negligible (Boros et al., 2013). Thus soda pans are groundwater discharge hotspots and surrounding local or regional higher lands are recharge zones of gravity-driven flow systems (Tóth, 2009), which can also be proved by the dissolved organic matters (DOM), distributed among the gravity-driven ground- and soda pan-waters (Boros et al., 2020). Based on these models, the contribution of surface inflow water to the P pool of soda pans is negligible. The external P loading has extensively been investigated in the groundwater wells in the region. The TP and SRP concentration data is available from the monitoring system of OVF (General Directorate of Water Management) in Hungary. The sum of 46 representative groundwater wells (depth up to 30 m) was selected from the database as reference for estimating the P content of groundwater. The wells are located farther than 1 km from settlements in the area where soda pans can be found in Hungary (Fig. 1). The mean of TP was 0.169 ± SD 0.187 mg/L and the SRP was 0.123 ± SD 0.158 mg/L (73% of TP) in these representative groundwater dataset.

The P loading of atmospheric precipitation fluxes was taken into account for as 21 mg P/m^2/year with 50% being SRP (Kopáček et al., 2011). It was estimated for the P loading of lakes in the Tatra Mountains as part of the Carpathian region, which is the nearest geographical location to the study area with available data (Fig. 1).

2.6. Data analyses

The statistical analyses were carried out in OriginPro 2021 (OriginLab, Northampton, MA, http://www.originlab.com) with significance levels of $p < 0.05$. Normality of variables and residuals were checked by Shapiro-Wilk and Kolmogorov-Smirnov tests and the variances were compared by Levene's and Brown-Forsythe tests. LN (X + 1) transformation was performed on the raw input data in order to normalise residuals except for the originally logarithmic pH.

We used the best fit non-linear exponential asymptotic ($y = a\text{-}b \times cx$) regression, which can be fitted by default models of Origin software to analyse the relationship between water depth and TP concentration for worldwide data (Table 3). The physico-chemical variables of the investigated soda pans were compared by Kruskal-Wallis ANOVA and Dunn's test among the soda pans. Pearson correlation and time series autocorrelation were computed on biweekly field data. Cross-correlation was calculated to analyse the significant forward or backward shift (time lag effects) between P loading of waterbirds and P-forms time series in the soda pans. Two-Way Repeated Measures ANOVA was performed for the experiment dataset with goose excrement and $NaHCO_3$ treatment factors for three P response variables (TP, TDP, SRP) with post hoc Tukey test were used for all pairwise comparisons of treatment units. The residual analyses were performed for regression and ANOVA, by Chi-Squared test of variance and Kolmogorov-Smirnov test of normal distribution fitting.

The cover of open water of the soda pans was mapped by RGB raster data of Sentinel 2 MSI sensor from 2017 via OpenLayers plugin by visual interpretation and manual screen digitalization technique. The GIS mapping procedure and spatial calculations were carried out using ArcMap (Environmental Systems Research Institute, 2013).

3. Results

3.1. Physico-chemical variables in the soda pans

The intermittent soda pans were very shallow (0–0.12 m) during the biweekly sampling period from April to November in 2017, and the Kelemen-szék pan completely dried out for a month between August and September. The salinity varied widely over the hypo- and mezosaline range (2040–27,760 mg/L), and the related pH was permanently alkaline (8.90–10.0). TP varied in an extreme hypertrophy range (1.45–23.0 mg/L), with a proportion of 67% TDP and 49% SRP of the TP by mean of three soda pans (Table 1).

3.2. Species composition and P loading of waterbird communities

The four main groups of waterbird communities can be identified based on the percentage contribution of P loading (g P/year) to soda pans in 2017. The most important groups were the geese and ducks (Anatidae) with 41.9%, the second was the gulls (Laridae, Sternidae) with 31.6%, while heron (Ardeidae, Ciconiidae, Threskiornithidae) and wader (Charadriidae, Recurvirostridae, Scolopacidae) species proportion was similar (10.2 and 10.1%). The crains (Gruidae) and cormorans

Table 1
Physico-chemical variables of the investigated soda pans in 2017.

Variables	Soda pans	N	Mean	SD	Minimum	Median	Maximum
Depth (m)	*Böddi-szék pan*	14	0.08	0.03	0.04	0.09	0.14
	Kelemen-szék pan	9	0.09	0.06	0.00	0.11	0.17
	Zab-szék pan	12	0.12	0.08	0.02	0.09	0.26
Salinity (mg/L)	*Böddi-szék pan*	14	**9951**	5675	4784	8792	23,280
	Kelemen-szék pan	9	**3561**	1702	2040	2640	7016
	Zab-szék pan	12	7415	6845	2848	5468	27,760
pH	*Böddi-szék pan*	14	9.54	0.21	9.08	9.57	9.78
	Kelemen-szék pan	9	9.35	0.32	8.90	9.37	9.83
	Zab-szék pan	12	9.62	0.21	9.24	9.63	10.01
TP (mg/L)	*Böddi-szék pan*	13	3.89	1.97	1.45	3.52	8.19
	Kelemen-szék pan	9	4.06	1.49	2.35	3.86	7.38
	Zab-szék pan	12	7.41	6.04	1.90	4.70	22.98
TDP (mg/L)	*Böddi-szék pan*	13	2.70	1.69	0.16	2.95	6.66
	Kelemen-szék pan	9	2.53	0.96	1.23	2.32	3.81
	Zab-szék pan	12	5.13	4.53	1.56	3.90	18.39
SRP (mg/L)	*Böddi-szék pan*	13	**1.82**	1.03	1.02	1.54	4.82
	Kelemen-szék pan	9	1.78	0.63	1.06	1.75	2.91
	Zab-szék pan	12	**3.95**	2.64	1.01	3.17	9.85
P loading of waterbirds (mg P/m^2/biweekly)	*Böddi-szék pan*	14	**12.06**	9.01	2.65	9.26	27.09
	Kelemen-szék pan	9	**5.08**	3.43	1.94	3.48	9.90
	Zab-szék pan	12	5.57	7.74	0.86	2.54	25.29

Note: significantly ($p < 0.05$) different means by Dunn's test are in bold.

(Phalacrocoracidae) contributed less (3.5 and 2.5%) to the P loading of waterbird community (Fig. 2).

The detailed species composition of P loading of waterbirds (g P/year) and percentage (%) on the soda pans in 2017 are summarized in Table S2. A total of seventy-five species were observed in 2017 on the three investigated soda pans and the composition of aquatic waterbird communities were similar, as indicated by the high proportion (63%) of identical species. The total phosphorus loading exceeded 1 g P/year in the case of twenty-four species, while only seven species and gulls, unidentified at the species level exceeded 10 g P/year on the average of the three soda pans. These were the nutrient importer herbivorous geese (*Anser albifrons*, *Anser anser*), omnivorous ducks (*Anas platyrhynchos*, *Anas crecca*) and gulls (*Chroicocephalus ridibundus*, *Larus michahellis*, *Larus cachinnans*) species. The total P loading volume of waterbird community ranged from 165,000,000 to190,000,000 mg P/year in the three study sites.

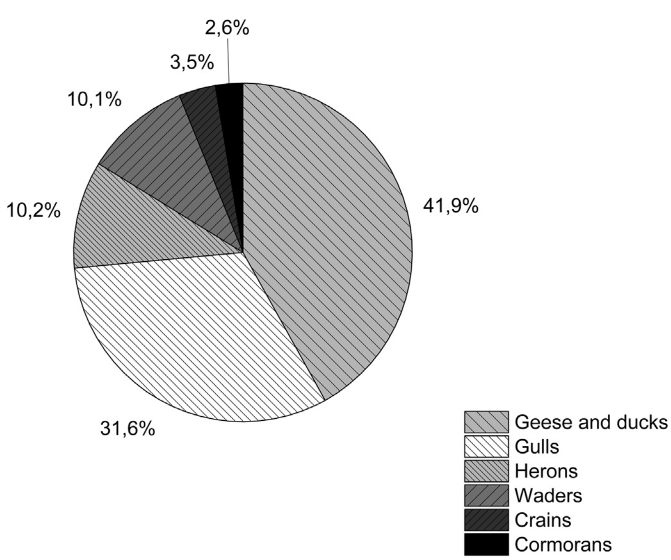

Fig. 2. Percentage composition of waterbird community by P loading (g P/year) on the soda pans in 2017, Taxonomic explanation: Geese and ducks (Anatidae) Gulls (Laridae, Sternidae) Herons (Ardeidae, Ciconiidae, Threskiornithidae) Waders (Charadriidae, Recurvirostridae, Scolopacidae) Crains (Gruidae) Cormorans (Phalacrocoracidae).

The P loading of waterbirds varied between 0.86 and 27.1 mg P/m^2/biweekly during the study period based on the biweekly estimation with a significant time series autocorrelation according to the seasonal trends of waterbird migration activity (Table 1, Fig. S1). There was a moderate peak in early spring due to goose and duck species, and there was another longer and higher peak in the fall migration season from August to November, with more waders and gulls in addition to the high density of geese and ducks (Table S2 and Fig. S1). The estimated total amount of surface-related P loading of waterbirds was 185 mg P/m^2/year (Böddi-szék: 332, Kelemen-szék: 89, Zab-szék: 135 mg P/m^2/year) and the volume proportional loading was 3.32 mg P/L/year (Böddi-szék: 5.21, Kelemen-szék: 2.06, Zab-szék: 2.70 mg P/L/year) on the average of the three soda pans.

3.3. Relationships between physico-chemical variables and P loading by waterbirds

The water depth for the three investigated soda pans (Fig. S2) varied as usual according to the intermittent hydrological cycle, which is one of the most significant environmental drivers in these ecosystems. The lowest water depth (a few centimetres) was observed between August and September, when the size of the water table was also the smallest. All variables negatively correlated with the water depth according to the inverse relationship between water volume and P concentration. All the investigated physico-chemical variables did not have a significant time series autocorrelation, which suggests their fluctuation has no evident trend. (Figs. S2–S4).

Salinity changed inversely to water volume in relation to water depth, with significant negative Spearman correlations (Table 2), with maximum variance (SD) in August and September at low water depth (Fig. S3), while the cross-correlation with $\pm$time shift lags did not estimate stronger relationship than direct correlation in relation with lack of time series trend (Figs. S2–S4).

All concentrations of P-forms showed a direct significant positive Spearman correlation with salinity, and pH also had a significant positive correlation with salinity according to their relationship in soda pans. The concentration of P-forms, such as TP, TDP, SRP, had a similar seasonal pattern to each other and varied significantly inversely with water volume in relation to water depth. An example of the seasonal pattern of TDP is shown in Fig. S4 where in August SD was at the highest, with the lowest water depth in the soda pans, and it had a significant direct Spearman correlation with water depth only (Table 2).

Table 2
The Spearman correlation matrix for the investigated variables of the soda pans in 2017.

Variables	Depth	Salinity	pH	TP	TOP	SRP	P loading of waterbirds
Depth	1.000	**−0.358**	**−0.463**	**−0.321**	**−0.345**	−**0.202**	**−0.567**
Salinity	**−0.358**	1.000	**0.587**	**0.542**	**0.658**	**0.510**	**0.373**
pH	**−0.463**	**0.587**	1.000	**0.582**	**0.585**	0.300	**0.379**
TP	**−0.321**	**0.542**	**0.582**	1.000	**0.881**	**0.777**	−0.113
TOP	**−0.345**	**0.658**	**0.585**	**0.881**	1.000	**0.877**	0.050
SRP	**−0.202**	**0.510**	0.300	**0.777**	**0.877**	1.000	**−0.159**
P loading of waterbirds	**−0.567**	**0.373**	**0.379**	−0.113	0.050	**−0.159**	1.000

Note: significant correlations are in bold.

Although there was no significant direct correlation between the concentration of P-forms (TP, TDP, SRP) and the P loading of waterbirds (Table 2), the significant shift indicated by cross-correlation with two-week time lags gave a better in situ estimation between the P loading and the P-forms of soda pans. The cross-correlation was increased with a lag of two weeks shift between the P loading of waterbirds and TP, with 1 lag shift $r = 0.322$, 2 lag shift $r = 0.369$. The cross-correlation increases slightly more between the P loading and TDP with two-week time lags as 1 lag shift $r = 0.349$, 2 lags shift $r = 0.486$, and between the P loading and SRP with two-week time lags as 1 lag shift $r = 0.370$, 2 lags $r = 0.436$.

The mean TP concentration (5.17 mg/L) of the soda pans exceeded with an order of magnitude (fifty-two times) the hypertrophic threshold (0.1 mg/L) of OECD (1982) fixed boundary system, after Vollenweider and Kerekes (1980). Apparently, the TP pool is not proportional with the specific loading and percentage contribution of the waterbirds on a worldwide scale respectively in different kind of referred ecosystems. We found that this is clearly inversely proportional to water depth and volume according to the following simplified equation based on the literature and our data (Table 3), which also includes the relevant data reported in this study (see also the negative correlation all of the variables with water depth in this study in Table 2):

$$\mathrm{LN\ (TP)} = 0.169\text{–}0.003^{\mathrm{LN\ water\ depth}} \quad (2)$$

$$\left(N = 23, \mathrm{df} = 20, r^2 = 0.876, p < 0.0001\right)$$

3.4. Release of P from goose excrement

The P loading of waterbirds was represented by Greylag Goose excrement factor in the ex situ laboratory experiment with doses of 1 and 2 g/L dry excrement treatment units, which resulted in significant P release in response variables at similar concentration as prevails in the soda pans TP: 2.35 and 3.99 mg/L, TDP: 1.60 and 2.54 mg/L, SRP: 1.21 and 2.11 mg/L. The composition of TP was very close to that of natural soda pans, with proportions of 65% TDP and 51% SRP in the mean of all treatments. The quantity of released P-forms used in the experiment was similar amount to the estimated in situ P loading of waterbirds and the concentration of P-forms predominant in soda pans. Furthermore,

Table 3
Comparable references of estimated surface- and volume related (mg P/m^2/year, mg P/L/year) P loading of waterbirds, contribution of the waterbirds to the total phosphorus pool (TP %), group of contributing waterbirds, affected habitats with the annual TP concentrations and some basic characteristic of the inland waters in the world.

Name of the site	Ha	Water depth mean (m)	TP mean (mg/L)	mg P/m^2/year	mg P/L/year	Waterbirds contribution to the TP (%)	Group of waterbirds	Habitat	Source
Lake Waban (USA)	360	4.80	0.045	8	0.002	0.4	Geese	Artificial pond	Moore et al., 1998
Goczalkowice Reservoir (Poland)	2754	5.20	0.267	35	0.007	1	All waterbirds	Reservoir	Gwiazda et al., 2014
Lake Arendsee (Germany)	514	28.60	0.163	438	0.015	88	Geese	Dimictic natural lake	Rönicke et al., 2008
Lake Grand-Lieu (France)	5150	1.20	0.394	45	0.038	5	All waterbirds	Freshwater flood	Marion et al., 1994
Green Lake (USA)	105	3.90	0.035	150	0.038	17	All waterbirds	Artificial pond	Scherer et al., 1995
Tata Old Lake	202	2.27	0.37	233	0.103	6	All waterbirds	Fishpond	Musicz, 2020
Swan Lake (Canada)	6	1.86	0.135	260	0.140	75	Geese	Gravel pit lake	Nürnberg and LaZerte, 2016
Greenfield Lake (USA)	37	1.30	0.145	230	0.177		All waterbirds	Reservoir	Mallin et al., 2016
Wintergreen Lake (USA)	15	2.40	0.198	587	0.244	70	Geese and Ducks	Glacial origin lake	Manny et al., 1994
Baton Rouge (USA)	4	1.20	0.408	350	0.292	8	Geese and Ducks	Artificial pond	Gremillion and Malone, 1986
Sósér pan (Hungary)	51	0.18	2.015	54	0.300		All waterbirds	Soda pans	Boros et al., 2016
Middle Creek Reservoir (USA)	162	1.00	0.131	520	0.520	93	Geese	Reservoir	Olson et al., 2005
Brown Moss (UK)	3	0.28	0.389	234	0.836	73	Geese and Ducks	Peat bog	Chaichana et al., 2010
Fuente de Piedra saline lake (Spain)	1350	0.35	0.270	331	0.946		Gulls and Flamingos	Saline lake	Martín-Vélez et al., 2019
Zab-szék pan (Hungary)	182	0.13	7.170	197	1.515		All waterbirds	Soda pans	Boros et al., 2016
Bosque del Apache wetlands (USA)	50	<1	2.379	1586	>1586	75	Geese	Wetland system	Post et al., 1998; Kitchell et al., 1999
Mean of Böddi-szék, Kelemen-szék, Zab-szék soda pans (Hungary)	89–148	0.10	5.2	185	1.907	65	All waterbirds	Soda pans	This study
Kelemen-szék pan (Hungary)	190	0.19	3.203	424	2.232	70	All waterbirds	Soda pans	Boros et al., 2008a
Zab-szék pan (Hungary)	182	0.19	5.706	615	3.237	70	All waterbirds	Soda pans	Boros et al., 2008a
Böddi-szék pan (Hungary)	198	0.14	2.619	578	4.129	70	All waterbirds	Soda pans	Boros et al., 2008a
Büdös-szék 2 pan (Hungary)	62	0.14	3.647	600	4.286	70	All waterbirds	Soda pans	Boros et al., 2008a
Büdös-szék 1 pan (Hungary)	70	0.14	6.412	748	5.343	70	All waterbirds	Soda pans	Boros et al., 2008a
Fehér-Lake pan (Hungary)	70	0.07	14.156	2500	35.714	70	All waterbirds	Soda pans	Boros et al., 2008a

Note: The volume-related unit (mg P/L/year) was calculated by surface-related P loading and the listed mean water depth (m) data.

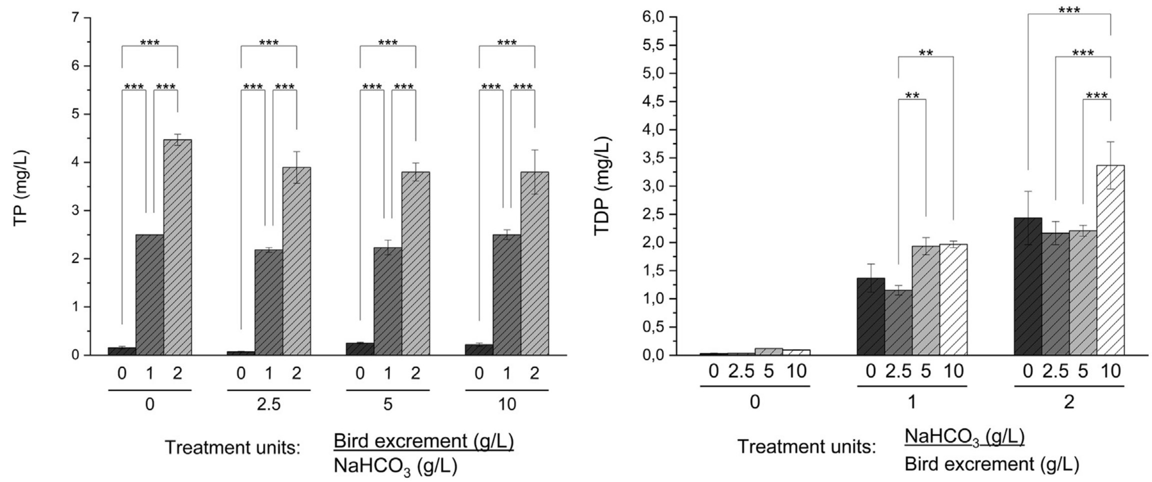

Fig. 3. a. Pairwise comparisons of released total phosphorus (mean ± SD) concentration as response variable in the treatment units by excrement factor (significances of Tukey test: $^{*}p \le 0.05$, $^{**}p \le 0.01$, $^{***}p \le 0.001$) b. Pairwise comparisons of released total dissolved phosphorus (mean ± SD) concentration as response variable in the treatment units by $NaHCO_3$ (soda) factor (significances of Tukey test: $^{*}p \le 0.05$, $^{**}p \le 0.01$, $^{***}p \le 0.001$).

the salinity range of treatments (1, 2.5, 5, 10 g/L) and the related pH also represented the chemical properties of natural soda pans (Table 1).

The results of Two-Way ANOVA for P response variables (TP, TDP, SRP) were significant by model ($F_{TP} = 347.222$, $F_{TDP} = 202.687$, $F_{SRP} = 347.222$, $p < 0.0001$) used factors as excrement ($F_{TP} = 1888.881$, $F_{TDP} = 1062.820$, $F_{SRP} = 1888.881$, $p < 0.0001$), $NaHCO_3$ ($F_{TP} = 4.736$, $F_{TDP} = 21.382$, $F_{SRP} = 4.736$, $p < 0.01$) and their interaction ($F_{TP} = 4.578$, $F_{TDP} = 6.630$, $F_{SRP} = 4.578$, $p < 0.005$) as well. Pairwise comparisons of all treatment units, including controls with Tukey tests indicated significant differences between all groups of excrement treatment (0, 1, 2 g/L) for all response variables (TP, TDP, SRP), which is represented by TP response variable in Fig. 3a. The $NaHCO_3$ treatment was significant between the 0–2.5 and 2.5–10 pairs of groups for TP response. Significant P release was observed in several cases between $NaHCO_3$ treatment groups, and the highest treatment response among the significant interactions was between 2.5 and 5 g/L, 2.5–10 g/L $NaHCO_3$ treatments in 1 g/L excrement units, and among 0–2.5–5–10 g/L $NaHCO_3$ treatments in 2 g/L excrement units in the case of TDP response variable which is represented in Fig. 3b.

3.5. Other external P loading

Comparing the estimated surface-related P loading of waterbirds (185 mg P/m^2/year, 3.32 mg P/L/year, 64% contribution to the TP) with the atmospheric precipitation fluxes referred as 21 mg P/m^2/year (0.219 mg P/L/year) with 50% part SRP (Kopáček et al., 2011) in the area, the precipitation contributes approximately 5% to the annual TP. Mean TP values (0.169 mg/L with 73% SRP) in groundwater monitoring wells (OVF) are reported to contribute about 3% to the annual TP in soda pans. As groundwater inflow typically exceeds surface-related watershed inflows and the amount of precipitation to soda pans (Simon et al., 2011; Boros et al., 2013), the P loading from watershed is almost negligible, estimated to contribute less than 3% to the total TP in the soda pan ecosystem.

4. Discussion

The estimated total amount of surface-related P loading of waterbirds (185 mg P/m^2/year) on the average of the three soda pans in 2017 represented a middle level of yearly amount. The volume-related P loading (3.32 mg P/L/year) was relatively high compared with worldwide references (Table 3), because of very shallow water depth (mean = 9.7 cm) during the investigation period, which draws attention to the distinction between the surface- and volume related P loadings. The average volumetric P loading of waterbirds (3.32 mg P/L/year) covered 64% of the average TP stock of soda pans (5.17 mg/L) in 2017, which is very close to the previously estimated value (70%) in this area (Boros et al., 2008a). Besides surface- and volume related P loadings can be highly variable in time and over the years in the Hungarian soda pans due to their multiple extreme endorheic environmental conditions (Boros et al., 2017) and fluctuating waterbirds population, this may even be the highest known value in the world for both surface and volume-related P loadings (2500 mg P/m^2/year, 35.71 mg P/L/year) as a guanotrophic indicator in aquatic ecosystems (Boros et al., 2008a, 2008b, 2016).

The second largest surface-related P loading of waterbirds (1586 mg P/m^2/year) was recorded in the Bosque del Apache wetlands (USA) with 75% contribution by geese (Post et al., 1998) to the hypertrophic pool of the TP, but it is less than it can be expected from P loading, due to the high flow rate of flood water from the Rio Grande River (Kitchell et al., 1999) (Table 3). The highest records of P loading of waterbirds (Fehér-Lake pan Hungary, Table 3) is equal to the P discharge of 500–700 persons/km^2 (high urbanized areas) human population density into the surface waters (Vollenweider, 1968; Morée et al., 2013).

Based on worldwide references, a wide range of types, size, depth, TP pool and waterbird contribution to the TP is available for comparison. Although not all waterbird species were involved in the different studies, all estimates took into account the most abundant and largest-bodied waterbirds in the study area. The surface-related P loading of waterbirds ranges in three orders of magnitude 8–2500 mg/m^2/year, and the estimated annual contribution of this amount to the total P loading of waterbirds is between 0.4 and 75%. It is clear that TP concentration is not always directly related to the P contribution of waterbirds in different aquatic habitats, but it is clearly inversely proportional to water depth (see Eq. (2) and Table 3 for details).

As Liu et al. (2014) experienced, the labile portion of waterbirds excrements can be readily dissolved in water and increase the level of inorganic nutrients within 3 days of excrements addition experiment. The result of our applied preliminary experiment showed that TP release peaked under laboratory conditions in one day at standard temperature (21 °C). Both the P loading of natural excrement by treatment and in situ estimated P loading of waterbirds with released concentration of P-forms in the experiment represented an equivalent range of P-forms that prevails in soda pans. In line with the ex situ laboratory experiment, in situ cross correlations with 2–4 week time lags suggest an estimate of a better relation between P loading and P-forms in soda pans, indicating a delay in dissolution of certain P-forms (e.g. particulate fractions) after P loading of waterbirds respectively. The nutrient and microbial dynamics of Fuente de Piedra saline lake (Málaga, Spain) showed a similar two weeks' time-lag with the abundance of flamingos (Batanero et al., 2017), which confirms our result. The released proportion of 65% TDP and 51% SRP of TP is very close to natural soda pans, which also proves the representativeness of the experiment.

The significant P release (especially for TDP) and interaction by goose excrement with $NaHCO_3$ treatment proves the importance of alkalinity (pH > 9 in $NaHCO_3$ treatments) contribution to the extreme hypertrophy TP pool in the soda pans. In line with our results, Krachler et al. (2009) found that the rate of decomposition was linearly related to pH in an organic matter decomposition experiment of a macrophyte (*Phragmites australis*) by incubation of air-saturated soda lake-water samples, suggesting that higher soda content and pH increase the mineralization of organic matter.

Although P is generally a limiting factor in the environment as it precipitates with calcium as a low solubility apatite mineral, and a strong accumulation of P in the sediment is common in eutrophic lakes, the sediment is frequently resuspended by wave action in shallow lakes, and pH increase can also lead to an increased phosphorus release from the sediment (Scheffer, 1998). The sediments in shallow aquatic systems and poorly drained soils (such as intermittent soda pan ecosystems), dry and re-flooding can be a source of high amounts of loosely absorbed P, causing recurrent internal eutrophication, rather than a sink of P in the lake sediment (Kinsman-Costello et al., 2016). Thus, the accumulation and resuspension of non-bioavailable forms is continuous in the water column, which keeps TP at a constant hypertrophic level, but primary production is lower than would be expected from TP, and the aquatic system appears heterotrophic, which is characteristic of soda pans (Vörös et al., 2008; Boros et al., 2016).

The total phosphorus and chlorophyll *a* relationship varies significantly according to several abiotic and biotic environmental factors as temperature, light, salinity, nitrogen and top down control (Hakansson and Eklund, 2010; Magumba et al., 2013; Filstrup and Downing, 2017). The correlation between the TP and chlorophyll *a* values of the soda pans of the Carpathian Basin demonstrates a broad variation of the Chlorophyll/TP ratio (Boros et al., 2017), but in spite of this variation there is a remarkable difference compared to most lakes in the world. Data plots and linear fit of soda pans by observed TP and Chlorophyll *a* relationship are below the OECD (1982) prediction with a few exception points (Fig. 4). In soda pans the average value of chlorophyll/TP ratio was 0.042, while in 'common' lakes it varied around 0.28–0.29 (Hakansson and Eklund, 2010). This remarkable difference suggests that the significant excess of phosphorus, due to the large proportion of directly available SRP, contradicts the limited primary production in these waters. However, the phytoplankton of these soda pans is likely to be limited by nitrogen, because the N/P ratio is usually significantly below the Redfield ratio (Redfield, 1934) in permanent alkaline soda pan ecosystems due to atmospheric ammonia (NH_3) emanations, which creates low N/P ratio and nitrogen limitation (Boros et al., 2008a; Clarisse et al., 2019), as well as high turbidity, which causes significant light limitation for phytoplankton (Boros et al., 2017). Petkuviene et al. (2019) found that algal growth was significantly greater when treated with piscivorous cormorant excrements than with predominantly herbivorous swan excrements, and heterotrophic bacteria were also stimulated by the addition of waterbirds excrements. Accordingly, not all P loading, dominated by herbivorous waterbirds will be available to aquatic organisms, and non-bioavailable forms can accumulate in these systems.

The average phosphate (calculated from SRP) concentration was approximately 0.083 mmol/L in the studied soda pans, which is far from the very high 0.1 M limit theoretically calculated by Toner and Catling (2020) for modern carbonate-rich lakes. This means that P accumulation state by guanotrophication in these intermittent ecosystems is limited, because periodic drying out can result in P loss, which also slows down eutrophication.

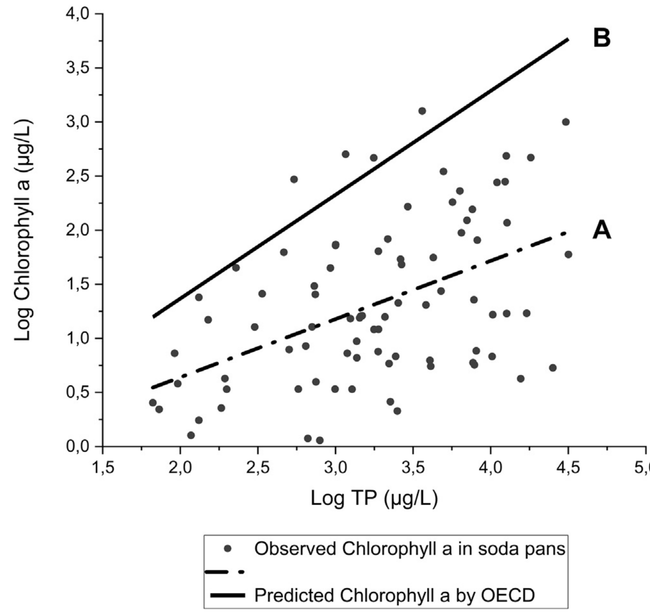

Fig. 4. Scatterplot and linear fit between observed concentration of total phosphorus (TP) and chlorophyll *a* in 84 soda pans in the Carpathian Basin (after Boros et al., 2017) with the predicted chlorophyll *a* by OECD (1982) model based on a large data set of world lakes legend: Line A) Log Chlorophyll $a = 0.538 \pm 0.108 \times$ Log TP $- 0.435 \pm 0.357$, $n = 84$, df $= 82$, $r = 0.482$, $r^2 = 0.232$, ***$p \leq 0.001$ Line B) Log Chlorophyll $a = 0.960 \times$ Log TP $- 0.553$ (OECD, 1982).

Overall, the results confirm the first hypothesis that the extremely high TP concentration of water in the soda pans is resulted by interaction of the characteristic physico-chemical properties of soda pans and P loading of waterbirds. The extreme hypertrophic level of TP is shaped by several factors: 1) one of the most important physical driver is shallow water depth according to Eq. (2); 2) the $NaHCO_3$ as the principal chemical component of soda pans causes a constant alkaline condition and enhances the release of dissolved P-forms from waterbirds excrements, 3) there is a high P loading of waterbirds causing guanotrophication proven by P release experiment and reliable estimation method of P loading.

5. Conclusion

The estimated high specific external P loading of waterbirds (mean: 185 mg P/m^2/y, 3.32 mg P/L/year) can explain the majority of the hypertrophic TP pool (mean: 5.17 mg/L, 64%) in soda pans, which is mediated by large-bodied herbivorous (geese and ducks) and medium-bodied omnivorous (e.g. gulls) waterbirds, who are important external nutrient importers and major phosphorus source. The results also confirm the hypothesis that groundwater (3%) and precipitation (5%) together account for a smaller estimated (8%) contribution to the hypertrophic TP pool in soda pans, while the contribution of waterbirds (64% in this study) to the TP is much higher (64–100%). In this study, the remaining part of TP (maximum 28%) pool can be explained by internal P sources, e.g. re-flooding and resuspension of sediment, benthic communities and macrophytes.

Soda pans are characterized by physical and chemical characteristics coupled with high densities of waterbirds, as biotic mediators of external P sources, which together cause the maintenance of high concentrations of P-forms. The extreme guanotrophication by high P loading of herbivorous waterbirds causing a hypertrophic state is in contradiction with the limited primary production of natural soda pans. This unique phenomenon can be explained by the multiple impact of prevailing extreme physico-chemical drivers (intermittent hydrological cycle, shallow water depth, high turbidity, salinity, alkalinity) and by the specific nutrient cycle of these alkaline soda ecosystems. The importance of the bio-availability of P-forms mediated by herbivorous waterbirds remains an open question in this environment.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.148300.

Data availability

All the basic data used can be found in Dryad depository at the following location for this dataset that is currently private for peer review: https://datadryad.org/stash/share/ctkhxkSdrb5aNcqsMa2CoRnlzQ6Qm_GMSqXk_MCx0RY

CRediT authorship contribution statement

Emil Boros: Conceptualization, Methodology, Field measurements, Experimental design, Data curation, Data analyses, Writing original draft, Editing, Supervision.

Anita Takács: Experimental design, Laboratory measurements, Editing.

Péter Dobosy: Experimental design, Laboratory measurements, Editing.

Lajos Vörös: Conceptualization, Methodology, Data curation, Data analyses, Validation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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