



Soils Drowned in Water Impoundments: A New Frontier

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Water impoundments have major impacts on biogeochemical cycles at the local and global scales. However, although reservoirs flood soils, their biogeochemical evolution below water and its ecological consequences are very poorly documented. We took advantage of the complete emptying of the Guerlédan Reservoir (Brittany, France) to compare the composition of soils flooded for 84 years with that of adjacent non-flooded soils used as reference, in 3 situations contrasted by their soil type (Cambisol and Podzol) and initial land-use (forest or grassland). In the annual drawdown zone, upper horizons of submerged soils are eroded, especially near the upper shore and on slopes. In the permanently drowned area, silty sediments cover drowned soils. Compared to reference soils, forest soils drowned for 84 years maintain their original morphological differentiation, but colors are dull, and the humus (O horizons) have virtually disappeared. Spodic horizons are depleted in poorly crystallized iron minerals while the accumulation of amorphous aluminum compounds remains unchanged. Soil bulk density increases as well as pH while total phosphorus content is almost unchanged. On the other hand, the pH of drowned grassland soils is lower by almost one unit, and the total phosphorus content was halved compared to reference soils. In this context, in addition to the effects of flooding, differences are attributed to post-1950 changes in agricultural practices i.e., liming and fertilization. Organic matter stocks decrease by almost 40%. This rate is similar in Cambisols and Podzols. Assuming that carbon was lost as CO₂ and CH₄, the corresponding flux averaged over the reservoir's life is close to global areal estimates of CO₂ emissions in temperate reservoirs and offsets a significant proportion of the carbon burial in reservoir sediments. Hence, flooded soils contribute significantly to the GHG budget of reservoirs, provide original long-term experimental sites to measure the effects of anoxia on soils and contain archives of past soil properties.

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INTRODUCTION

Since ancient times, water reservoirs have been built to supply cities with drinking water, irrigate agricultural land, prevent devastating floods, facilitate navigation or produce mechanical or electrical energy (Bordes, 2010; French Committee on Dams and Reservoirs (CFBR), 2013). The major rivers of Europe and the United States were dammed during the twentieth century. In addition,

small dams are extremely numerous. As a result, the present land area flooded in reservoirs and ponds is about 340,000 km² (Downing et al., 2006). Many dams are presently being completed in Canada, Asia, Africa, and South America, and it is planned that the number of large reservoirs will double by 2040 (Zarfl et al., 2015) collecting about 90% of the world's stream and river flow (Van Cappellen and Maavara, 2016). With the prospect of a warming climate, the construction of many additional small ponds is currently being considered for irrigation, fish farming, drinking water supply, snow production, etc...

Because they increase water residence time (Vörösmarty et al., 1997), decrease oxygen concentration (Friedl and Wüest, 2002), store sediment (Vörösmarty et al., 2003), carbon (Dean and Gorham, 1998; Cole et al., 2007) and nutrients (Maavara et al., 2014, 2015), and release GHG (Deemer et al., 2016), impoundments have major impacts on biogeochemical cycles at the local and global scales (Billen et al., 1991; Maavara et al., 2017). In addition, water reservoirs flood soils, which are gradually covered with sediments. Properties of soils temporarily submerged have been thoroughly studied (Ponnamperuma, 1972; Sahrawat, 2003). But very few studies have been focused on the soils drowned below meters of water in reservoirs. Yet the study of such soils raises new scientific questions and has ecological applications.

Drowned soils could provide information about soils of the past, if the morphology and properties of the original soils are preserved. The challenge is to explore these archives from varied ages and to compare them with the properties of present soils, as has been done with buried soils for instance (Valentine and Dalrymple, 1976).

However, flooding drastically changes the soil environment. Soils drowned below water become anoxic and get gradually covered by sediments. This drastically reduces the input of biological carbon to the soil, as well as bioturbation. When oxygen is available, decomposition of organic matter (OM) in water is faster than in air, because microbial growth is not limited by drought (Kristensen et al., 1995). In the absence of oxygen, labile carbon is mineralized as rapidly as in the presence of oxygen (Kristensen et al., 1995; Bastviken et al., 2004). But complex macromolecules such as lignins are more slowly degraded (Canfeild, 1994; Kristensen et al., 1995; Bastviken et al., 2004) especially because the activity of white rot fungi is reduced (Medeiros et al., 2009; Cornut et al., 2010). In the absence of oxygen, Fe and Mn become more labile, as do compounds that are chemically bound to them, such as phosphorus and organic matter. Due to the major role of poorly crystallized minerals in OM stabilization (Rasmussen et al., 2018), this might a major driver of flooding impact on soil carbon balance. The mobility of these compounds and bioproducts are influenced by the chemical properties of the water in the reservoir and by the movements of water at the water-sediment-soil interface, which depend on reservoir management.

The evolution of flooded soils may have consequences on the ecological dynamics of reservoirs: (a) the observation of emptied reservoirs shows that soils are eroded in the drawdown zone, and contribute to sediment accumulation (Maleval, 2010; Félix-Faure et al., 2018); (b) carbon and nutrients contained in flooded soils

TABLE 1 | Main features of the Guerlédan reservoir.

Reservoir main features							
Impoundment year	1931	Dam length (m)	208				
Altitude (m asl.)	124	Dam height (m)	45				
Area (km ²)	3.07	Input mean annual discharge $(m^3.s^{-1})$	10.74				
Length (km)	7.5						
Volume (hm ³)	52.6	Input mean february discharge $(m^3.s^{-1})$	23.2				
Max depth (m)	43						
Mean depth (m)	20	Input mean august discharge (m3.s-1)	2.34				
MRT (day)	56						
Watershed area (km²)	620	Power (GWh.yr ⁻¹)	20				

(and vegetation) may contribute to the trophic upsurge phase (Turgeon et al., 2016), which leads to an increase in the biological productivity of the reservoir following flooding; (c) this evolution may also lead to the anoxia of deep layers in the reservoir and to a pulse in greenhouse gas (GHG) emissions (Barros et al., 2011; Prairie et al., 2017) after impoundment.

To evaluate the fate and ecological impact of flooded soils, we took advantage of the exceptional emptying of the Guerlédan Reservoir, which is located on the Blavet River (Brittany, France). This reservoir covers different geological substrates and land uses, with specific soil types, within the same topographic and climatic context.

Our objectives were: (1) to compare the morphology and geochemistry of flooded soils in the different drawdown zones, in comparison to non-flooded reference soils located in the immediate vicinity of the reservoir. (2) To quantify the change in soil organic matter and nutrient stocks after flooding. (3) To evaluate the potential release of carbon from drowned soils in reservoirs, at the local and global scale.

MATERIALS AND METHODS

Study Site

General Characteristics

The reservoir of Guerlédan is located in Brittany, Northeastern France, in the Blavet valley. The elevation of the reservoir is 124 m asl. The average air temperature is 12°C, and the average annual rainfall is 1,060 mm. The local watershed is mainly covered with meadows, crops, and a few forests.

A 45-meter-high dam was built and the reservoir was impounded in 1931. Its main tributary, the Blavet, has a mean annual discharge of $10.7~{\rm m}^3.{\rm s}^{-1}$. The reservoir is 7 km long and floods the Blavet valley and the old canal from Nantes to Brest in the bottom. The main physical characteristics of the reservoir are presented in **Table 1**.

The reservoir consists of two parts (**Figure 1A**):

- A main basin formed by the Blavet valley, from the hamlet of Bonrepos (downstream of Gouarec) to the dam. The vegetation is mainly composed by oak coppices, with *Pteridium aquilinum* and *Polytrichum formosum*, on gentle slopes (<15%). On the southern shore, soils are Albic Podzols developed on quarzitic sandstone. The geological basement

of the northern shore, is formed of shale (Middle or late Ordovician). The soils are Entic Podzols below forest areas, while Cambisols are associated with grasslands and crops.

- A shallow bay (maximum depth: 16 m), connected by a narrow arm to the main basin, northeast of the dam. This bay collects water from small tributaries that drain meadows and crops with a gentle slope (<10%). The littoral soils are Cambisols developed from shale.

Based on the criteria of Hakanson (1980), the Guerlédan Reservoir is meso-eutrophic. In 2013, the average annual DOC, nitrate and total phosphorus concentrations were 4.4 mg C.l⁻¹, 6.66 mg N-NO₃.l⁻¹, and 0.036 mg P.l⁻¹, respectively. The average concentration of chlorophyll a was 7.75 μ g.l⁻¹, and the depth of the Secchi disc varied seasonally between 1.6 and 3.5 m. Surface water pH varied seasonally from 6.8 in winter to 8.4 in summer, and bottom water pH varied from 6.8 to 8.0 (Agence de l'Eau Loire-Bretagne, 2018).

Water Level Variations

Three drawdown zones have been defined according to the variations in the water level in the reservoir:

- The annual drawdown zone is between the maximum water level in the reservoir (124.3 m asl.) and the elevation of 121 m. Between 1986 and 2016, water level fluctuations occurred in this zone for 89% of the time.
- The occasional drawdown zone is the area between 121 and 117 m asl. Between 1986 and 2016, water level fluctuations occurred in this zone for 7% of the time.
- The permanently drowned area is located between the elevation of 117 and 81 m asl. The water level fell within this zone only during the complete emptying of the reservoir, which took place in 1951, 1966, 1975, 1985, and 2015.

Sampling

We selected toposequences on the same geological basement, with similar former land use inside the reservoir and present land use outside the reservoir. Land use data before the impoundment of the reservoir, in 1931, was obtained from the land cadastre of 1920 (Council of the department of Côtes-d'Armor, 2015; Department of Morbihan, 2015). This information, and the geological map (scale 1:50,000), allowed three main landscape units to be selected: forest on sandstone, forest on shale, and meadow on shale. The streambed area and areas strongly modified by man (canal and banks, quarries, houses, roads, etc...) were avoided (Figure 1A).

To cover the diversity of geological substrates, soil types, and land use, three transects perpendicular to the littoral slope were chosen: one transect covering forests on Albic Podzol (sandstone), one transect covering forests on Entic Podzol (shale) and one transect covering grassland on Cambisol (shale). Each transect started with a reference site 10–20 m upstream from the reservoir and continued with sites in the annual drawdown zone (0–1 depending on the transect) and permanently drowned zone (one in the Cambisol and the Entic Podzol transects, and three in the Albic Podzol transect).

Soil sampling was done in the summer of 2015, during the complete emptying of the reservoir. The soil at each site was described and sampled horizon-by-horizon from a soil pit (except for the reference site of the Cambisol which was sampled with the root auger). At the same elevation, five soil cores were collected along a 10 m-long transect arranged perpendicular to the slope, but only two of the three flooded sites of the Albic Podzol transect were investigated. The root auger used (8 cm in diameter and 15 cm long, for a total collection volume of 754 cm³) allowed soil bulk density and stone content to be measured down to a depth of 30 cm or 45 cm below the O horizon (for reference soils) and below the sediment cover for the drowned soils.

The sediments deposited on the surface of the flooded soils were sampled separately using the root auger. The distinction between sediments and the superficial horizon of flooded soils was clear in terms of color, texture and soil structure.

The O horizons ($O_L + O_F + O_H$) of forest soils on shale (Entic Podzol) and sandstone (Albic Podzol) were sampled entirely using a 0.04 m² frame (20 * 20 cm square). Five replicates were made at each site, along a line perpendicular to the general slope.

The locations and details of the samples are summarized in **Figures 1A,B** and in **Table 2**, respectively.

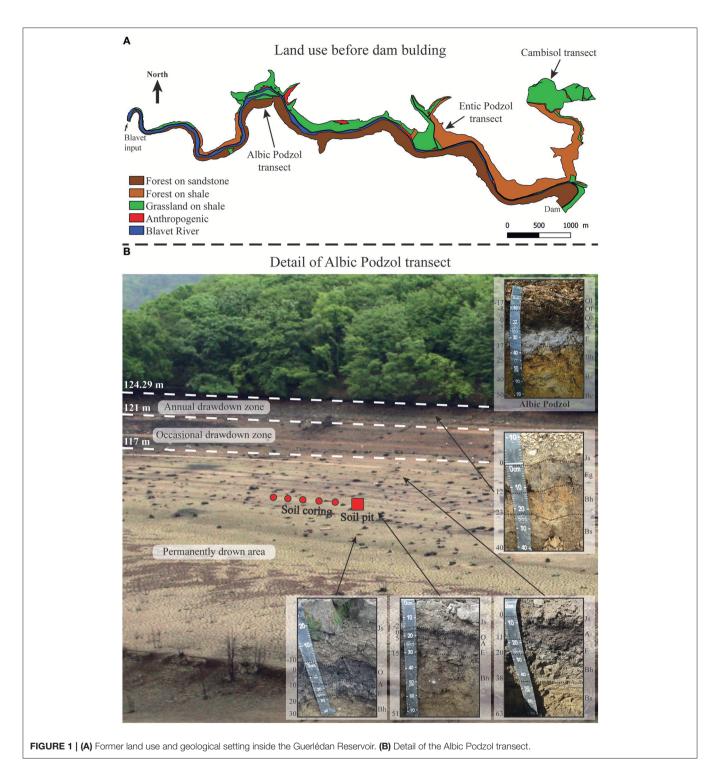
Analysis

Soil and sediment samples were air-dried and sieved to measure the weight of coarse elements ($>2\,\text{mm}$). Humus samples (O horizons) were dried and weighed after removing large roots ($\emptyset > 5\,\text{mm}$).

With few exceptions, soil samples collected by horizon followed the same analytical protocol performed at the central soil analysis laboratory of INRA, following ISO or French standards: 5 fractions particle-size analysis (NF X 31-107); pH in water (ISO 10390); total phosphorus (NF X 31-147); total organic carbon (ISO 10694); total nitrogen (ISO 13878); amorphous iron (Amorph-Fe) and aluminum (Amorph-Al) extracted by oxalate, following (Tamm, 1922); and iron not bound to silicates, extracted by a dithionite-citrate system buffered by sodium bicarbonate (DCB-Fe), following (Mehra and Jackson, 1960). The iron oxide (Fe-oxide) content was computed by subtracting Amorph-Fe from DCB-Fe. Measurements of cation exchange capacity and base saturation by the cobaltihexamine method (NF X 31-130) were performed on 15 samples.

Soil cores sampled by depth were used to measure the bulk density and coarse element content after drying (40°C for 24 h) and sieving (<2 mm); it was assumed that the coarse elements had a density of 2.6. After grinding in an agate mortar, the total carbon and nitrogen contents of the fine earth as well as their isotopic composition ($\delta^{13}C$ and $\delta^{15}N$) were measured with an elemental analyser (vario Isotope cube, Elementar,) connected to an isotope ratio mass spectrometer (IsoPrime 100) at the isotope analysis platform of INRA Nancy.

From soil analyses carried out on the samples according to depth (5 replicates per depth), carbon and nitrogen stocks in the 0–15, 15–30, and 30–45 cm soil layers (except for the Albic Podzol where the layer 30–45 cm was not sampled) at each site



were computed according to the following equation:

$$Stock = (Da^*[C])^*(1 - (Vol_{CE}/Vol_{sample}))^* H_{sample}$$

Da: bulk density of the fine soil (g.cm $^{-3}$); [C]: total organic carbon (or total nitrogen) content of the sample (%); Vol_{CE}: volume (m 3) of coarse elements (>2 mm) of the sample, obtained from the mass and a theoretical density of 2.6; Vol_{sample}: total

volume of the sample (m^3) ; H_{sample} : height (m) of the sampled core. Only three measurements of coarse element content were performed at the drowned Albic Podzol sites. When values were missing, stocks were computed with reference soil values.

Carbon stocks of flooded soils were also calculated using a mass of mineral soil (soil mass corrected by subtracting the OM mass) equivalent to the reference soil. The deepest layer of the flooded soil was artificially truncated or extended to reach an equivalent total mineral soil mass of reference soil.

TABLE 2 | Main features of transects, sites and associated sampling effort.

Transect			Sites		Sampling		
Soil type	Bed rock	Soil occupation	Mean slope (%)	Elevation (m)	Drawdown zone	Horizon by horizon	Replicated cores by depth
Cambisol	Shale	Grassland	5 (4–7)	130	Reference	-	Х
				114	Permanently flooded	X	X
Entic Podzol	Shale	Forest	20 (15-25)	130	Reference	X	X
				122	Annual drawdown zone	-	X
				110	Permanently flooded	X	X
Albic Podzol	Sandstone	Forest	11 (10–15)	130	Reference	X	X
				122	Annual drawdown zone	-	X
				114	Permanently flooded	X	-
				110	Permanently flooded	X	X
				106	Permanently flooded	X	X

RESULTS

Soil Morphology in Relation to the Drawdown Zones

Figure 1B shows the Albic Podzol transect on sandstone, as well as the morphology of the soils in the reference zone, the annual drawdown zone and the permanently drowned area.

In the reference littoral zone, the slope is \sim 15%. The soil presents the characteristic sequence of Albic Podzol horizons: Mor-type humus (O), thick (20 cm); A horizon (5 cm thick), very dark brown (7.5YR2.5/2); E horizon (12 cm), grayish brown (10YR5/2); Bh horizon (8 cm), black (5YR2/1); Bs horizon (15 cm), yellowish red (5YR4/6), and strong brown (7.5YR5/8); and Bc horizon (10 cm), light brown (7.5YR6/3).

The transition between the forest area and the reservoir is marked by a vertical step, \sim 1 m high.

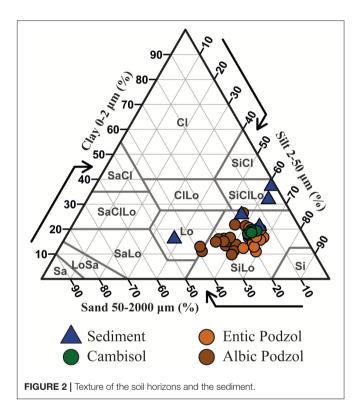
In the annual drawdown zone, at the elevation of 122 m asl, on a slope of \sim 15%, the soil surface is paved with a few centimeters of gravel. Below this horizon occurs a small discontinuous Eg horizon (possible ghost of the former E horizon). The Bh and Bs horizons can still be identified, but have bleached colors.

In the permanently drowned area, drowned soils are covered by dark grayish brown silty sediments (Js) (10YR4/2) with a lamellar structure. This layer, 10–30 cm thick, lies over an organic horizon consisting of a darker upper part [O, black (10YR2/1), rich in organic fragments (roots, twigs)] and a lower part [A, dark grayish brown (10YR4/2)]. The E horizon is identifiable, but of gray color (10YR6/1). The spodic horizons are brown (10YR5/3) to brownish yellow (10YR6/8).

Observations along the other transects on Entic Podzol and Cambisol confirm these evolutions: the upper part of soils (O and A at least) in the annual drawdown zone is truncated; soils in the permanently drowned area are discolored compared to references. Pseudogley spots are absent or very discrete.

Particle-Size and Texture Classes

The texture (**Figure 2**) of the soils in the different transects is silt-loam (USDA). The clay content varies between 26.5 and 9.8%, with an average of 16.5 \pm 3.5%. No change was observed along the slopes. The Albic Podzol horizons developed from sandstone



are slightly sandier (mean: $25.9 \pm 5.3\%$, min: 19.2%, max: 32%). The upper horizon of the soils of the annual drawdown zone is characterized by a higher content of coarse sand, 16 and 24% for the sites on Entic Podzol and Albic Podzol, respectively.

In the transects on Entic Podzol and Cambisol, the content of coarse elements (>2 mm) is higher in the reference soils upstream than in the submerged profiles located in the middle or lower slopes. In the Albic Podzol, the coarse element content of drowned soils is unknown in the 0–15 cm layer, and slightly higher in the 15–30 cm layer than in the reference soil (**Table 3**).

By comparison, the sediment texture in the permanently drowned area varies between loam upstream and silt-clay-loam downstream. The sediments do not contain coarse elements.

TABLE 3 | Average coarse element content in reference and drowned soils by depth for each transect.

Transect	Depth	Coarse elements (g/100g)				
		Reference soil	Flooded soil			
Entic Podzol	0-15 cm	15 ± 2	6 ± 2			
	15-30 cm	15 ± 3	8 ± 4			
	30-45 cm	12 ± 3	9 ± 4			
Albic Podzol	0-15 cm	26 ± 15	- *	- *		
	15-30 cm	11 ± 3	(15.7) **	(16.2; 15.4) **		
Cambisol	0-15 cm	14 ± 5	8 ± 1			
	15-30 cm	21 ± 7	9 ± 9			
	30-45 cm	20 ± 7	4 ± 2			

Mean values are given in g/100 g \pm sd. *: Coarse element content was not measured; reference soil values were used for stock calculations. **: Coarse element content was measured for only three samples, given in parentheses. When values were missing, stock calculations were performed with reference soil values.

Bulk Density

In the transects under forest, the fine earth bulk density of the reference soils increases from 0.6 in the 0–15 cm layer (Entic Podzol: 0.6 \pm 0.1, Albic Podzol: 0.7 \pm 0.2) to 1 in the spodic horizons (1.0 \pm 0.1 in the 30–45 cm layer of the Entic Podzol and 1.1 \pm 0.3 in the 15–30 cm layer of the Albic Podzol). In drowned soils, the bulk density is on average slightly higher: 0.7 \pm 0.2 and 1.0 \pm 0.1 in the 0–15 cm layers; and 0.9 \pm 0.1 and 1.3 \pm 0.0 in the spodic horizons of the Entic and Albic Podzols, respectively.

Under grassland, the bulk density of the reference Cambisol varies from 1.0 \pm 0.1 at 0–15 cm to 1.2 \pm 0.1 at 15–30 cm and 30–45 cm. By comparison, the drowned soil bulk density is 1.2 \pm 0.1 in the 0–15 cm layer, but 1.1 \pm 0.1 in the 15–30 cm and 30–45 cm layers.

Organic Matter

Carbon Content (Figures 3A,B)

The carbon contents of the reference forest soils are 9.7, 3.6, and 2%, respectively, in the A, Bh, and Bs horizons of the Entic Podzol and 13.9, 3.0, and 2.6%, respectively, in the A, Bh, and Bs horizons of the Albic Podzol. The carbon contents of the O horizons are close to 40% (not shown on the graph).

In the drowned soils, the evolutions diverge. For the Entic Podzol, the carbon content in the A horizon (14.2%) is higher than that in the reference, whereas the carbon content has changed little in the spodic horizons (Bh: 4.1% and Bs: 1.8%). However, comparing the 5 replicates sampled by depth, differences between drowned (0–15 cm: C = 5.2 \pm 2.0%) and reference (0–15 cm: C = 6.0 \pm 1.0%) soils are not significant, because of high variability especially in the drowned soils.

For the Albic Podzol, the carbon content is much lower in drowned soils than in the reference, in the A horizon (6.3%) and in the spodic horizons (Bh: 0.8%, Bs: 0.5%). However, differences between drowned and reference soils are not significant in the 5 replicates sampled by depth, because of high variability especially in the reference area.

The carbon contents of the grassland reference soil are lower (3.2, 1.8, and 1.0%) in the 0–15, 15–30, and 30–45 cm layers, respectively) than in reference forest soils. The carbon contents of drowned soils are significantly lower (1.7, 1.1, and 0.7%) in the 0–15, 15–30, and 30–45 cm layers, respectively) than in the reference soils.

C/N Ratio

The C/N ratios of the reference soils differ widely in relation to soil type and land use (**Figures 3C,D**), with values of \sim 10 in the Cambisol, 20 in the Entic Podzol and 27 in the Albic Podzol. The C/N ratio of the O horizon is above 40 (46 \pm 2 and 41 \pm 2 for the Entic and Albic Podzol, respectively).

Under forest, in the Entic Podzol, the C/N ratios of the drowned site (A horizon: 31; Bh: 50; Bs: 23) are higher than in the reference. In the three Albic Podzol drowned sites, the C/N ratio of the A horizons (39 \pm 7) is higher, while the C/N ratio of the spodic horizons (Bh: 15 \pm 3 and Bs: 12) is lower than that of the reference. However, differences between drowned and reference soils are not significant in the 5 replicates sampled by depth (except a higher value at depth 15–30 cm of the Entic Podzol), because of high variability especially in the drowned area.

The C/N ratio in the drowned Cambisols is significantly higher by about one unit at all depths than in the reference.

Soil $\delta^{13}C$ and $\delta^{15}N$

Under forest, in the Entic Podzol, the average $\delta^{13}C$ is $-28.3 \pm 0.2\%$ in the O horizon and increases from $-27.4 \pm 0.3\%$ to $-26.2 \pm 0.1\%$ with increased depth. The $\delta^{13}C$ of drowned soils follows a parallel pattern but is shifted by ~ 1 unit downward. Conversely, the $\delta^{15}N$ values of the reference and drowned soils are very close and increase from ~ 3.5 to 4.5% with increased depth. In comparison, the $\delta^{15}N$ of the O horizon is $-6.2 \pm 0.7\%$ (Figures 4A,B).

The evolution of soil $\delta^{13}C$ in the Albic Podzol is rather similar, but the difference between the reference soil and drowned soils is much less (\sim -0.3‰). The depth variation in soil $\delta^{15}N$ is also rather similar (4.0 \pm 0.7‰ at 0–15 cm to 4.5 \pm 1.5‰ at 15–30 cm), but the $\delta^{15}N$ of drowned soil is lower by 0.5 to 1‰ (**Figures 4C,D**).

Under grassland, the Cambisol δ^{13} C increases from $-28.4 \pm 0.3\%$ to $-26.4 \pm 0.3\%$ with increased depth. The evolution is similar in the drowned soil, but the δ^{13} C of the 0–15 cm layer is one unit higher ($-27.5 \pm 0.0\%$). The δ^{15} N values of the reference and drowned soils are similar and close to 6.5%, except in the 30–45 cm layer of the drowned soil, where δ^{15} N is lower (5.1 \pm 0.4%) (**Figures 4E,F**).

Soil Carbon Stocks

The carbon stocks (Cstock) in the O horizons of the Entic and Albic Podzols are 44 ± 8 tC.ha⁻¹ and 41 ± 17 tC.ha⁻¹, respectively. Below the O horizons, the Cstock values measured down to 45 and 30 cm depths in the Entic and Albic Podzols are 97 ± 4 and 83 ± 19 tC.ha⁻¹, respectively. In total, the Cstock values are estimated at 141 ± 10 and 124 ± 29 tC.ha⁻¹, respectively. In comparison, Cstock values in the drowned soils

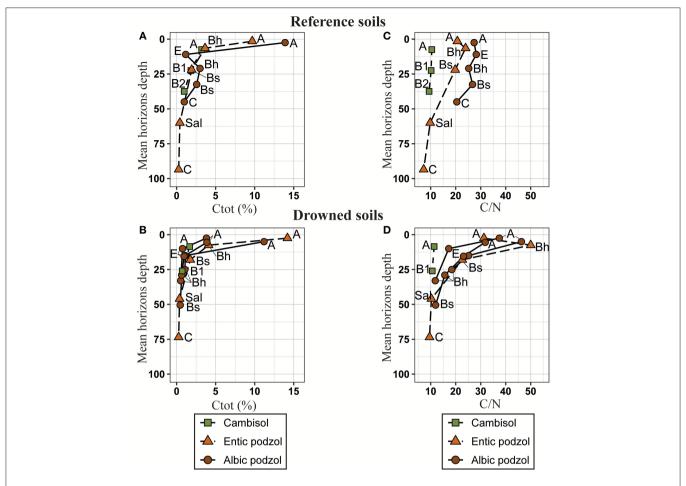


FIGURE 3 | Total organic content (Ctot) of the horizons of reference soils (A) and drowned soils (B). Carbon/nitrogen (C/N) ratio (wt/wt) of the horizons of reference soils (C) and drowned soils (D). Holorganic horizons are not shown. Green square: Cambisol. Orange triangle: Entic Podzol. Brown dot: Albic Podzol. Horizon names are specified beside each point.

are 87 ± 18 tC.ha⁻¹ for the Entic Podzol and 81 ± 7 tC.ha⁻¹ (0–30 cm) and 77 ± 16 tC.ha⁻¹ (0–30 cm) for the two Albic Podzol sites (**Figures 5A,C**).

In the grassland, Cstock down to the depth of 45 cm is 88 ± 8 tC.ha⁻¹ in the reference soil and 58 ± 3 tC.ha⁻¹ in the drowned soil (0–45 cm) (**Figure 5E**).

Computing stocks in drowned soils for a mass of mineral soil equivalent to that of the reference soil does not change much the results: 86 ± 24 tC.ha $^{-1}$ in the Entic Podzol, 75 ± 7 tC.ha $^{-1}$ and 71 ± 14 tC.ha $^{-1}$ for the two Albic Podzol sites respectively and 54 ± 2 tC.ha $^{-1}$ in the Cambisol (**Figures 5B,D,F**).

By comparison, the sediment Cstock calculated on a layer of 15 cm was 6 \pm 2 tC.ha $^{-1}.$

Nitrogen Stocks (Figures 6A-C)

The total nitrogen stocks in the O horizon are 1.0 \pm 0.2 tN.ha⁻¹ and 1.0 \pm 0.5 tN.ha⁻¹ for the Entic and Albic Podzols, respectively.

Below the O horizons, the cumulative nitrogen stocks measured down to 45 and 30 cm depths in the Entic and Albic

Podzols are 4.4 ± 0.3 tN.ha⁻¹ and 3.2 ± 0.6 tN.ha⁻¹, respectively. Including the O horizons, the stocks are 5.4 ± 0.4 tN.ha⁻¹ and 4.2 ± 0.8 tN.ha⁻¹, respectively. In comparison, the cumulative nitrogen stocks in the drowned soils are 3.5 ± 0.9 tN.ha⁻¹ for the Entic Podzol and 3.3 ± 0.3 tN.ha⁻¹ and 2.9 ± 0.4 tN.ha⁻¹ for the two Albic Podzol sites.

In grassland, the nitrogen stocks down to the depth of 45 cm in the reference and drowned soils are 8.8 ± 0.7 tN.ha⁻¹ and 5.1 ± 0.3 tN.ha⁻¹, respectively.

Geochemical Evolution

Hq

The reference soil pH decreases from the Cambisol to the Albic Podzol (**Figures 7A,B**). Under forest, soil pH increases with depth, from ~4 in the A horizon to 5 in the BC horizon. Under grassland, pH increases from 5.6 to 6.2 with depth.

The pH of all drowned soils is between 4.5 and 5 in the upper layer and between 5.5 and 6 at depth. Under forest, the pH of drowned soils is approximately one unit higher than that for reference soils. Conversely, under grassland, the pH of the

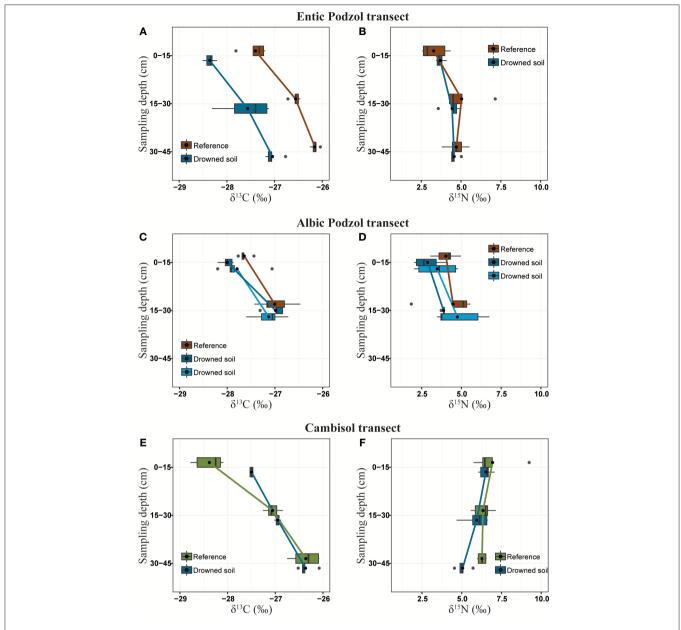


FIGURE 4 | Boxplot of the isotopic ratios (δ^{13} C and δ^{15} N) of soil sections. (**A,B**) Entic Podzol transect. (**C,D**) Albic Podzol transect. (**E,F**) Cambisol transect. At each depth, gray dots are outliers and black dots are averages; data for the same soil are connected by lines.

drowned soil is nearly one unit lower than that for the reference: this higher pH of the reference soils is confirmed by the level of exchangeable calcium relative to the cation exchange capacity (CEC) in the 0–15 cm layer: 4.7 cmolCa.kg $^{-1}$ for a CEC of 5.7 cmolCa.kg $^{-1}$ in the reference, but 1.4 cmolCa.kg $^{-1}$ for a CEC of 2.2 cmolCa.kg $^{-1}$ in the drowned soil.

Total Phosphorus

In reference soils, the total phosphorus (Ptot) content differs widely depending on land use and soil type (**Figures 7C,D**). Concentrations are 3 to 5 times higher under grassland (1.3% to

0.9%) than under forest, and in forest soils, values are the lowest in the Albic Podzol.

In drowned soils under grassland, Ptot concentrations are half that in the reference, while concentrations in soils under forest do not differ from those of reference soils.

Amorphous Iron and Crystallized Iron Oxides

The evolution of oxalate-extracted iron (Amorph-Fe) in reference soils follows the redistribution of amorphous iron associated with the podzolization process (**Figure 8A**). In the Albic Podzol, the Amorph-Fe content is lowest in the A and E horizons (<0.1%) and highest in the Bh and Bs horizons (1.3 and

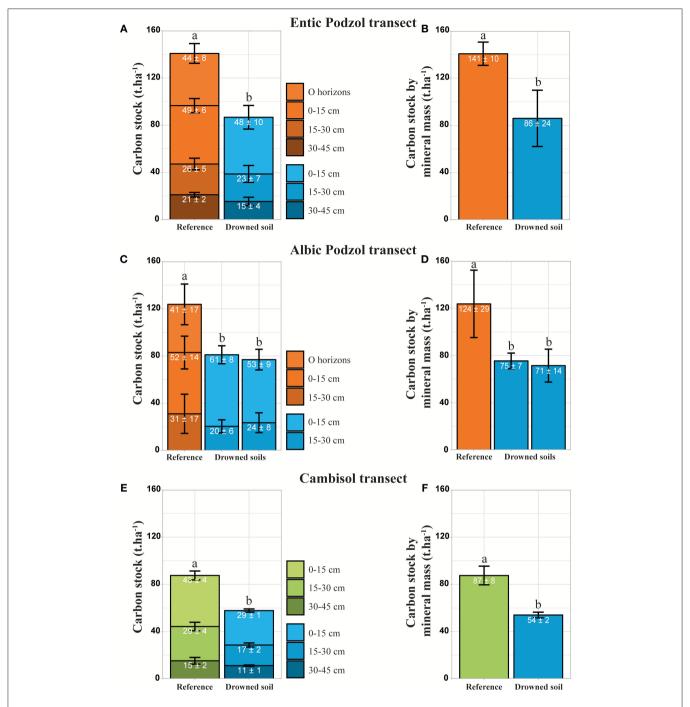


FIGURE 5 | (A,C,E): Bar plots of the average total organic carbon stocks $(t.ha^{-1})$ by depth, down to 45 cm for Entic Podzol and Cambisol and 30 cm for Albic Podzol (see text). Error bars represent \pm 1 sd. Average stock values at each depth are given \pm 1 sd. (B,D,F): Bar plots of average organic carbon stocks $(t.ha^{-1})$ calculated for a mass of mineral soil equivalent to the reference soil. Error bars represent \pm 1 sd. Average stock values at each depth are given \pm 1 sd. Statistical differences were calculated by transect using TukeyHSD test. Entic Podzol: p-values < 0.01. Cambisol: p-values < 0.01.

2.5%, respectively). This vertical differentiation is less marked in the Entic Podzol (A: 0.6%, Bh: 1.3%, and Bs: 0.9%) and is lacking in the Cambisol (A: 0.7%, B_1 : 0.7%, and B_2 : 0.5%). The CDB-Fe content follows a similar distribution with lowest values in the A horizons of Podzols (Albic: A: 0.2% and Entic: A: 2.1%) and

highest values in spodic horizons (Albic: Bh: 1.6%, Bs: 3.1%, and Entic: Bh: 3.2%, Bs: 3.2%). The CDB-Fe content in the Cambisol is homogenous down to 45 cm (A: 1.7%, B₁: 1.9%, and B₂: 1.8%). The contents in iron oxides (CDB-Fe–Amorph-Fe) (**Figure 8C**) is depleted in the A and E horizons. The iron oxide content of

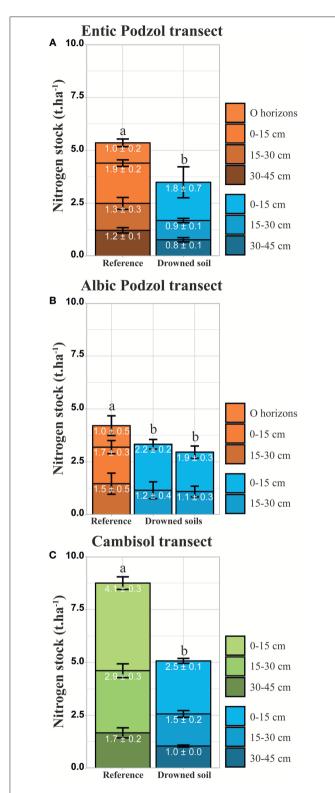


FIGURE 6 | Bar plots of the average nitrogen stocks (t.ha $^{-1}$) by depth, down to 45 cm for Entic Podzol **(A)** and Cambisol **(C)** and 30 cm for Albic Podzol **(B)** (see text). Error bars represent \pm 1 sd. Average stock values at each depth are given \pm 1 sd. Statistical differences were calculated by transect using TukeyHSD test. Entic Podzol: p-values < 0.05. Albic Podzol: p-values < 0.05. Cambisol: p-values < 0.01.

deep horizons in the Albic Podzol derived from sandstone (0.5%) is much lower than that of Cambisol and Entic Podzol derived from shale (1.5%).

For comparison, the Amorph-Fe and CDB-Fe contents of the fine sediment covering the soils are 1.0 \pm 0.2% and 1.5 \pm 0.1%, respectively.

In drowned soils, the amorphous Fe content of all soil (Figure 8B) horizons converges to values between 0.2 and 0.5% without vertical differentiation (except one Albic Podzol site with a content of 0.8% in the A horizon). In the Albic Podzol, compared to the reference, contents slightly increased in the A and E and strongly decreased in Bh and Bs. The iron oxide contents of the drowned and reference Albic Podzol are low and very close. The contents in the drowned soils on shale (0.8%) are lower (Cambisol) and much lower (Entic Podzol) than in the reference (Figure 8D).

Oxalate-Extracted Aluminum

In the reference soils, the evolution of oxalate-extracted aluminum (Amorph-Al) follows the redistribution of iron associated with the podzolization process. Horizon A samples in the forest soils are poor in Amorph-Al, with values of 0.1 and 0.3% in the Albic Podzol and Entic Podzol, respectively. Spodic horizons are richer, with values of 0.3 and 0.6% for Bh and 0.7 and 0.7% for Bs in the Albic Podzol and Entic Podzol, respectively. The Cambisol Amorph-Al contents are 0.25, 0.25, and 0.27% in horizons A, B₁, and B₂, respectively.

In general, the content of Amorph-Al in drowned soils has changed little, apart from a notable decrease in the Bs horizon of Albic Podzol at one site.

DISCUSSION

Soil Erosion in the Annual Drawdown Zone

In the annual drawdown zone, along the three transects and independent of slope, all O and A horizons have disappeared. Soils are truncated down to a depth that we could reconstruct from the surface soil level around tree stumps and for the height of the soil step surrounding the reservoir. An average soil loss of about 40 centimetres' depth may have affected weak slopes (<10%). On steeper slopes, and especially near the maximum water level, all soil down to the C horizon has been eroded by waves. Residual coarse elements from soils in the annual drawdown zone cover the surface of soils downstream and slow their erosion. In the occasional drawdown zone, superficial horizons are reworked and mixed with sandy sediment originating from upstream.

Evolution of Drowned SoilsOrganic Matter Changes and GES Emission

The O horizons of drowned soils have almost entirely disappeared. The spatial homogeneity of the A horizons of drowned soils suggests that they were not eroded. Erosion would most likely have left ghosts, protected by stumps or roots, which we did not observe. In addition, we found fragments of small roots or branches on the upper limit of the A horizon in the Podzol profiles. These fragments suggested relicts of O horizons.

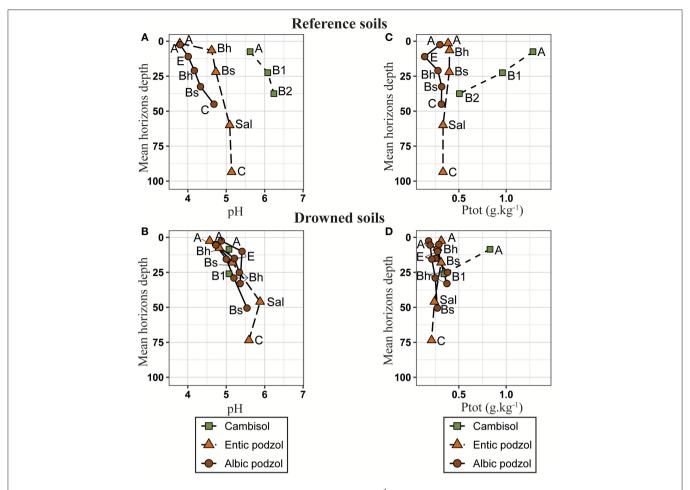


FIGURE 7 | pH_{water} of the horizons of reference soils (A) and drowned soils (B). Ptot (g.kg⁻¹) of the horizons of reference soils (C) and drowned soils (D). Holorganic horizons are not shown. Green square: Cambisol. Orange triangle: Entic Podzol. Brown dot: Albic Podzol. Horizon names are specified beside each point.

Partial dispersion and erosion of the litter layer (O_L horizon) when the reservoir was flooded cannot be excluded. But it should be kept in mind that the O_F and O_H layers are densely prospected by roots, which certainly prevents erosion. The higher C/N of the drowned Podzol A horizons compared to that of the reference soil might be explained by a carbon input from the original O horizon. Lateral variability in C content and C/N was very high, both in the drowned and reference areas, and within horizons and depths. Because of this high variability, the difference in carbon contents between control and drowned sites were not significant. Changes in carbon stocks were mostly related to the disappearance of the O layer. However, comparing total C stocks, differences were highly significant.

After being drowned for 84 years under water, and considering a mass of mineral soil equivalent to that in the $\{O \text{ horizon} + 0-45 \text{ cm}\}$ layer of the reference soil, the Cambisol, and Entic Podzol have lost 36 and 39%, respectively, of their initial carbon stock, that is between 3.3 and 5.5 kgC.m⁻², respectively. Calculated over a thickness of 30 cm, the Albic Podzol has lost on average 41% of its initial carbon stock, that is 5.4 kgC.m⁻².

Although of lower magnitude, these proportions are comparable to that (50%) measured using the same method in Cambisols under meadows drowned for 80 years in another reservoir of the Massif Central (Félix-Faure et al., 2018). The rate measured in the Cambisol might also be compared to that measured in long-term terrestrial experiments. Menichetti et al. (2014) showed in five 30- to 80-years-long bare fallows that soils kept with no vegetation had lost 33–65% of their carbon. It suggests that permanent submersion of soils, in probably anoxic conditions, does not drastically reduce long-term carbon mineralization rates.

In drowned forest soils, decreases in carbon stocks are greatest in the upper layers: O horizon + 0–15 cm: 48 and 39% on average for Entic Podzol and Albic Podzol, respectively. The most likely reason of this important decrease is a relatively high content of labile organic matter in O and A horizons. The increase in the C/N ratio of the A horizons may be related to (i) the input of organic matter with a C/N > 40 from the O horizons. Carbon loss from the spodic horizons of the Podzols could be facilitated by the removal of iron associated with illuvial organic matter. On the

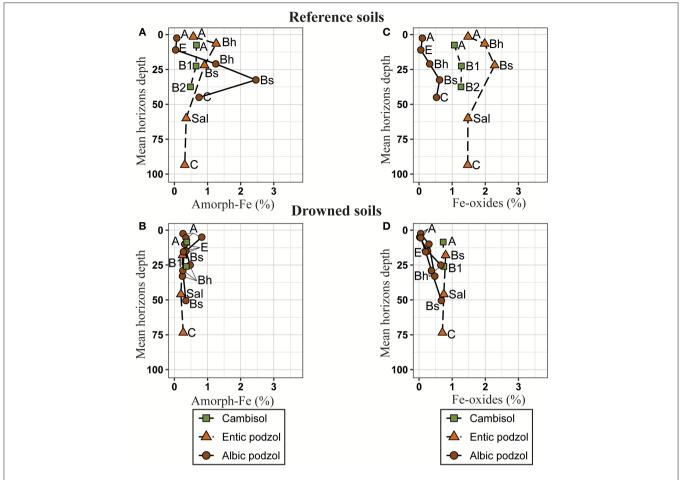


FIGURE 8 | Oxalate-extracted iron (Amorph-Fe) (%) of the horizons of reference soils (A) and drowned soils (B). Iron oxides (Fe-oxides) (%) of the horizons of reference soils (C) and drowned soils (D). Holorganic horizons are not shown. Green square: Cambisol. Orange triangle: Entic Podzol. Brown dot: Albic Podzol. Horizon names are specified beside each point.

other hand, for the Cambisol, the lower C/N of current grasslands is likely related to their high level of nitrogen fertilization.

The surprising fact that almost similar organic matter losses were measured in Podzols and Cambisols may be explained by the rise in pH of acid soils in contact with the waterbody. In fact, carbon and nitrogen mineralisation might have been directly affected by the change in pH (Rousk et al., 2009), indirectly by the alteration of the mineral phases that protect carbon (Rasmussen et al., 2018). It may be noticed that most of the carbon lost from Podzols is from the humus layers, that is from relatively fresh organic matter, whereas the Cambisol loses carbon from all depths.

Another explanation is related to the availability of oxygen. Oxygen saturation profiles in water in relation to depth measured close to the dam (Electricité De France, 2014) show that the water column is oxic in winter and spring. In summer and autumn the oxygen content decreases to almost 0 mg.l⁻¹ in the thermocline (depth between 7 and 12 m, that is approximately at the elevation of 115–110 m asl). Most of our drowned soil samplings are within this zone. The oxygen content increases

below the thermocline in relation to the entry of oxic water from the main stream (Blavet). This means that for the Albic Podzol, which is located upstream, water might be oxic all year round, whereas water might be anoxic in autumn in the Entic Podzol area (see Figure 1A). In the shallow bay, where the Cambisol transect is located, the oxygen content might also be higher in relation to water level fluctuations.

In addition, sediment interstitial water composition was measured (Electricité De France, 2014). In the area of the Albic Podzol, the $\rm NH_4/NO_3$ ratio in sediment water varies between 0.35 upstream and 11.4 downstream. In the area of the Entic Podzol, nitrate is almost absent ($\rm NH_4/NO_3=26$). Hence oxygen availability might explain why mineralization went deeper in the profile in the Albic Podzol (C losses from the Bs) compared to the Entic Podzol. The same process might have influenced decomposition in the Cambisol area.

The evolution of $\delta^{13}C$ is paradoxical. Indeed, atmospheric $\delta^{13}C$ has decreased for the past century as a result of the combustion of fossil fuel (Suess effect). Hence, independent of all other processes, the surface horizons of present soils should

be depleted by approximately one delta unit relative to their equivalents 80 years ago (Graven et al., 2017). If one adds to this the isotopic enrichment associated with the loss of young organic matter (Balesdent and Mariotti, 1996; Menichetti et al., 2014), an enrichment of more than one delta unit in favor of the drowned soils is foreseeable. The observation made on the 0-15 cm layer of the Cambisol is consistent with this, although the difference is <1 unit, and agrees with previous observation of (Félix-Faure et al., 2018) in drowned Cambisols below grasslands. On the other hand, the $\delta^{13}C$ values of the 15–30 and 30–45 cm layers are not different from those of the drowned soils. It should be kept in mind that the historical change of organic fertilization practices may contribute to these figures. We know that silage corn has been widely used as livestock feed by Breton farmers for the past 30 years: this could lead to manures, and soils, enriched in 13 C. In addition, δ^{15} N values are very high for all the profiles, which could be attributed to high manure fertilization for the current grassland and potentially to nitrogen mineralization for the drowned soil.

However, under forest, we observe the opposite of what the Suess effect should produce. The δ^{13} C of drowned soils is less than that of the current forest profile, with a value of more than one unit over the entire profile of Entic Podzol and less than half a unit in Albic Podzol. Several factors could be involved in reducing the δ^{13} C of drowned soils. (1) The reference soil upstream of the toposequence is richer in coarse elements and therefore drier. Balesdent et al. (1993) showed a decrease of two units in δ¹³C in tree leaves and soils along a toposequence of the Paris basin ranging from a drier plateau to a wetter bottom. Applied to the studied toposequence, a difference in moisture along the slope could account for some of the observed difference. (2) In addition, it is known that lignin is particularly conserved during anaerobic mineralization because the activity of white rot fungi is depressed in the absence of oxygen. As lignin is depleted in ¹³C compared to bulk organic matter (Benner et al., 1987), this could lead to a lower δ^{13} C in drowned soils subjected to differential mineralization of their organic matter. And a difference in oxygen availability (see above) might explain the larger Δ^{13} C in the Entic Podzol. However, this pattern was not observed by Oelbermann and Schiff (2008) during their flooded soil mineralization experiment. This "anomalous" isotope pattern would deserve further investigation.

These figures provide a framework for considering the effects of soil flooding on greenhouse gas emissions by reservoirs. Flooded soils provide carbon to the water body, most likely in the form of $\rm CO_2$ and $\rm CH_4$, which finally reaches the atmosphere. The time dynamic of carbon release is not known, but it is likely that most of the losses occur before the soils are covered by a continuous layer of sediment, that is, during the first 25 years following impoundment. We did not compute precisely the loss of carbon from eroded soils in the drawdown area, but we may conservatively assume a similar loss than in the permanently drowned soils (\pm 40%) even if the loss rate is probably much faster, especially for the organic horizons (Blodau and Moore, 2003). This flux may explain the statistical (Barros et al., 2011) and experimentally measured (Abril et al., 2005) peak in GHG emissions and further decline following the flooding

of reservoirs. In fact, if we divide the weighted average soil carbon losses measured on a reservoir area basis (3.9 kgC.m $^{-2}$) by 25 years, and assume that the losses correspond to a gaseous emissions, this would lead to an average emission, by flooded soils, of about 430 mgC.m $^{-2}$.d $^{-1}$. In comparison, the mean CO₂ emission rate of temperate reservoirs given by Barros et al. (2011) is about 350 mgC.m $^{-2}$.d $^{-1}$, and, globally, young (<20 years) reservoirs emit about 4 times more than old ones. From the process point of view, Kim et al. (2016) used a terrestrial biochemistry model (DNDC), modified to take into account redox conditions in drowned soils, to simulate C emissions from a forest Podzol in Canada. They computed an average emission of 1.4 gC.m $^{-2}$.d $^{-1}$ for the first 5 years after flooding. Our data and samples could be used to experimentally calibrate this model over the long term.

On the other hand, the global carbon sink associated to reservoir sediment, given by Mendonça et al. (2017) is 0.06 Pg.yr⁻¹ for a global area of 3.5 10⁵ km², that is about 400 mgC.m⁻².day⁻¹. Although crude, this comparison suggests that the carbon storage in reservoir sediments may be balanced by the carbon released form drowned soils during the first decades after flooding.

Geochemical Evolution, Legacies, and Historical Change

Compared to current podzolized forest soils, the drowned soils maintain morphological podzolic differentiation, but the colors are dull. The redistribution of amorphous Al, characteristic of the podzolization process, is preserved. On the other hand, the vertical redistribution of amorphous iron disappears. The release of most of the amorphous iron under low redox conditions probably explains the absence of characteristic colors and spots of gley. Redox conditions in drowned soils may also explain the decrease in iron present in the form of oxide (CDB-Fe minus Amorph-Fe) in the soil profiles developed from shale, under forest or meadow. This decline was not observed in the Albic Podzol developed on sandstone, but the initial concentrations were much lower than those in other soils.

What is the fate of the iron removed from soil profiles? A fraction might accumulate in the A and possibly E horizons, in the vicinity of the soil-sediment interface, as suggested by the observed increase in the Amorph-Fe content of these horizons. This redistribution would be responsible for the homogenization of the contents in the drowned soil profiles. Another fraction of this Amorph-Fe would migrate to the reservoir water body through the sediment. The Amorph-Fe content of the sediment is in fact on average twice as high as those of the drowned soils. The monitoring of the complete emptying of the Guerlédan Reservoir in 1985 indicated high levels of dissolved iron (0.1 to 3 mg.l⁻¹) in the water collected at the end of the complete emptying (Electricité De France, 2014). The discharge of red-colored water containing soluble iron during the first years after reservoir filling as well as after complete reservoir emptying has already been described in tropical reservoirs (Chanudet et al., 2016).

The higher pH of drowned forest soils in relation to that of the reference is most likely related to loss of organic matter and

to the contact with reservoir water, whose pH varies between pH 6.6 and 7.4 near the bottom (Electricité De France, 2014). The higher pH in the "reference" Cambisol under meadow is most likely linked to the evolution of agricultural practices in the past 70 years. Liming of agricultural land, especially grassland, is extremely unlikely before the 1960s (Coppenet, 1983), as there is no limestone in the bedrocks of Brittany. Only marl collected from sea shores was used. Large scale liming was initiated in the eighties, and soil pH was regionally raised since 3 then. Hence, before 1931, soils were certainly more acidic than nowadays. The low Ptot contents of forest soils vary very little in relation to flooding. However, as observed for carbon, an increase in the Ptot content in the A horizon should be seen if some phosphorus originally present in the O horizons of soils accumulates in the A horizon. This was not observed, which suggests that the organic phosphorus present in the O horizon was released to the water body, or to the sediment. Under grassland, total phosphorus levels in the drowned soil are low relative to those in the reference grassland, and the difference is mostly in the 0-15 and 15-30 cm layers. As regards liming, P fertilization of grasslands in Brittany before the 1950s is highly unlikely. The meadow soils drowned in 1931 had most likely never been fertilized, while the current grassland used as a reference has most likely been fertilized. In the same way, the high density of the 15-30 cm layer of present

grassland, which is not found in flooded soils, could be due to a plow sole. These examples provide a glimpse of the type of information that can be expected from such underwater archives but also the difficulties inherent in this exercise.

Hence, drowned soils contribute significantly to the GHG budget of reservoirs, provide original long-term experimental sites to measure the effects of anoxia on soils and contain archives of past soil properties. For these reasons, they deserve extra attention.

AUTHOR CONTRIBUTIONS

JF-F, CW, VC, and ED conceived and planned the experiments. JF-F, CW, VC, J-NA, CH, and ED contributed to sample preparation. JF-F performed the calculations. CW, JB, VC, and J-MB aided in interpreting the results. JF-F and ED wrote the manuscript with input from all authors.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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