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LETTER

Enhanced greenhouse gas emission from exposed sediments along a hydroelectric reservoir during an extreme drought event

Hyojin Jin\textsuperscript{1,4}, Tae Kyung Yoon\textsuperscript{1,4}, Seung-Hoon Lee\textsuperscript{3}, Hojeong Kang\textsuperscript{1}, Jungho Im\textsuperscript{1} and Ji-Hyung Park\textsuperscript{1}

\textsuperscript{1} Department of Environmental Science and Engineering, Ewha Womans University, Seoul 120-750, Korea
\textsuperscript{2} School of Civil and Environmental Engineering, Yonsei University, Seoul 120-749, Korea
\textsuperscript{3} School of Urban and Environmental Engineering, Ulsan National Institute of Science and Technology, Ulsan 689-798, Korea
\textsuperscript{4} These authors contributed equally.

\textbf{E-mail:} jhp@ewha.ac.kr

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Abstract

An active debate has been underway on the magnitude and duration of carbon (C) emissions from hydroelectric reservoirs, yet little attention has been paid to stochastic C emissions from reservoir sediments during extreme climatic events. A rare opportunity for field measurements of CO\textsubscript{2} efflux from a hydroelectric reservoir in Korea during an extreme drought event was used to examine how prolonged droughts can affect microbial organic matter processing and the release of CO\textsubscript{2}, CH\textsubscript{4} and N\textsubscript{2}O from exposed sediments. Chamber measurements of CO\textsubscript{2} efflux along an exposed sediment transect, combined with high-frequency continuous sensor measurements of the partial pressure of CO\textsubscript{2} (pCO\textsubscript{2}) in the reservoir surface water, exhibited extraordinary pulses of CO\textsubscript{2} from exposed sediments and the turbulent inflowing water in contrast to a small CO\textsubscript{2} sink in the main water body of the reservoir and a low efflux of CO\textsubscript{2} from the flooded sediment. Significant increases in the production of CO\textsubscript{2}, CH\textsubscript{4} and N\textsubscript{2}O observed in a laboratory incubation of sediments, together with enhanced activities of phenol oxidase and three hydrolases, indicate a temporary activation of microbial organic matter processing in the drying sediment. The results suggest that drought-triggered pulses of greenhouse gas emission from exposed sediments can offset the C accumulation in reservoir sediments over time scales of years to decades, reversing the trend of declining C emissions from aging reservoirs.

1. Introduction

Lakes and reservoirs are important sources of C evasion from inland waters to the atmosphere; recent estimates of the global CO\textsubscript{2} evasion from standing water systems range from 0.32 to 0.53 Pg C yr\textsuperscript{-1} (Tranvik \textit{et al} 2009, Raymond \textit{et al} 2013). Hydroelectric reservoirs account for 25% of the global area used for artificial freshwater systems, yet their role as a C source has been underappreciated (Barros \textit{et al} 2011, Hu and Cheng 2013). Large C emissions from flooded soils and vegetation following dam construction can offset the reduction of greenhouse gas (GHG) emission associated with hydroelectricity generation (Giles 2006, Fearsndise and Pueyo 2012, de Faria \textit{et al} 2015). Although CO\textsubscript{2} and CH\textsubscript{4} emissions from hydroelectric reservoirs have been suggested to comprise a small fraction of the global C evasion from inland waters (Barros \textit{et al} 2011), uncertainties remain unresolved regarding spatiotemporal variations in the production and consumption of CO\textsubscript{2} and CH\textsubscript{4} across seasons and reservoir components (Fearsndise and Pueyo 2012, Hu and Cheng 2013). While high GHG production in flooded vegetation and soil organic matter usually occurs during the initial flooding phase (Abril \textit{et al} 2005, Teodoru \textit{et al} 2010), C evasion rates can also increase drastically in drawdown areas in response to periodic flooding and draining (Chen \textit{et al} 2009, Hu and Cheng 2013). Little attention has been paid to changes in GHG emissions from seasonally exposed bottom sediments along the reservoir and its inflowing tributaries.
There is a growing interest in the emissions of CO$_2$ and other GHGs from dried streambeds of temporary or ephemeral watercourses, particularly in arid areas (Gallo et al 2014, von Schiller et al 2014). It has been well established that droughts can release C stored in peats by enhancing aeration in waterlogged peats in which the availability of oxygen constrains phenol oxidase, minimizing the activity of other hydrolytic enzymes responsible for organic matter decomposition (Freeman et al 2001, Fenner and Freeman 2011, Wang et al 2015). In contrast, studies that investigated desiccation effects on the bacterial community in streambed sediments have often shown decreases in microbial functions such as extracellular enzyme activity (Amalfitano et al 2008, Marxsen et al 2010, Pohlon et al 2013). Some of these studies have suggested desiccation-induced shifts in the streambed bacterial community composition toward increasing dominance of Actinobacteria and Alphaproteobacteria over desiccation-vulnerable Gram-negative bacteria (Marxsen et al 2010, Pohlon et al 2013).

Recent increases in the frequency and intensity of droughts, as observed in arid areas of North America, have been attributed to global warming (Overpeck 2013, Williams et al 2015). Although much attention has been paid to drought impacts on the water storage and electricity production of hydroelectric reservoirs, little efforts have been made to investigate drought impacts on the carbon balance of hydroelectric reservoirs, resulting in a dearth of direct field measurements of C emissions from the reservoir water and sediments. To examine drought impacts on C emissions from reservoir sediments, we combined field and laboratory measurements of sediment GHG emissions and microbial activities with satellite remote sensing of the affected reservoir surficial area in the Lake Soyang, the largest hydroelectric reservoir in South Korea that was built in 1973 to provide electricity and flood control. We used a rare opportunity for field measurements of reservoir pCO$_2$ and sediment CO$_2$ effluxes during the peak of the most severe drought since dam construction. The field measurements were complemented with a laboratory incubation for estimating production potentials of CO$_2$, CH$_4$ and N$_2$O and measurements of sediment enzyme activity and microbial composition to examine potential mechanisms for enhanced C emissions from drought-exposed sediments.

2. Methods

Lake Soyang is the deepest and largest reservoir in South Korea (37°56′44″N, 127°48′52″E; figure 1) with a maximum depth of 110 m near the dam and a total watershed area of 2700 km$^2$ (Lee et al 2013; refer to supplementary information for more detailed descriptions on the study site and methods). The reservoir has a dendritic shape, consisting of the primary axis that is 60 km long and 0.5 km wide and many lateral branches. The reservoir is oligo-mesotrophic, with relatively small inputs of domestic and industrial wastewater, but agricultural runoff from expanding croplands on the steep mountainous terrain has been increasing in recent decades (Park et al 2010, Lee et al 2013).

Continuous measurements of water pCO$_2$, water temperature and light intensity at 1 min intervals were conducted at 20 cm below the surface of the reservoir near the dam from 8 June through 22 June 2015. The atmospheric pCO$_2$ was not measured at the study site, so we used concurrent measurements from a downstream (~150 km) river site. The atmospheric pCO$_2$ was measured at the height of 1 m above the river surface (Yoon et al 2016). The pCO$_2$ was measured by a diffusion-type, non-dispersive infrared (NDIR) CO$_2$ sensor (GMT222, Vaisala, Finland) enclosed in a water impermeable, gas permeable polytetrafluoroethylene (PTFE) membrane tubing (International Polymer Engineering, USA) (Johnson et al 2010). The efflux of CO$_2$ from the reservoir surface was calculated using measured differences of pCO$_2$ between air and water and an estimated gas transfer velocity (Raymond et al 2013).

On the day when pCO$_2$ measurements near the dam were completed, CO$_2$ efflux was measured along a 200 m transect established over a large area of exposed sediment (>200 m wide) in an upper reach of the main reservoir channel, 36 km upstream of the dam (figure 1). We used a metallic, flow-through soil gas flux chamber connected to a CO$_2$ analyzer (LI 820, LI-COR, USA) to determine CO$_2$ efflux associated with both autotrophic and heterotrophic respiration from the water surface of flooded sediment along the margin of water channel (sampling points A: turbulent water 60 cm off the margin; B: very shallow water along the margin), recently exposed, moist sediments (C and D) and drier sediments vegetated with grass species (E and F). At each of the six transect locations, three replicate measurements were conducted at 1 m intervals along a line perpendicular to the transect.

Surface sediment samples (~5 cm) were collected by using a metal corer (inner diameter: 5 cm; depth: 5 cm) from the same transect. Samples were immediately transported to the laboratory and a portion of each sediment sample was frozen for real-time polymerase chain reaction (PCR) analysis. A portion of each homogenized sample was oven-dried at 60 °C for 48 h, and the gravimetric soil water content was determined by measuring the ratio of weight loss from drying against the dry weight. To measure production potentials of CO$_2$, CH$_4$ and N$_2$O approximately, 20 g of fresh sample was placed in 120 ml vials and the vials were then sealed with gas-impermeable butyl septa and aluminum crimps (Wheaton, USA) and incubated at 20 °C for 48 h. The gas concentrations in the
headspace air samples collected at 0, 24 and 48 h were measured by a gas chromatograph (7890A, Agilent, USA) fitted with a Supelco Hayesep Q 12 ft 1/8″ column. After confirming that all three-point measurements showed linear increases, the increase in gas concentration over the 48 h incubation period was converted to the amount of each gas produced from a unit area of 5 cm deep sediment based on the ideal gas law and the ratio of soil mass to the area of the sediment corer (Holland et al 1999).

The activity of four representative soil enzymes including phenol oxidase, β-glucosidase, N-acetyl glucosaminidase and phosphadase was determined with sieved and homogenized surface (depth: 5 cm) sediment samples within two days from the sampling. Although oxygenation of surface sediment might have differed across the sampling transect, our measurements of enzyme activity in the bulk sediment of 5 cm depth would represent an average condition prevailing in the surface sediment of each sampling location.

L-DOPA was used to measure the phenol oxidase, whereas methylumbelliferyl (MUF)-β-D-glucopyranoside (MUF-G), MUF-N-acetyl-β-D-glucosaminide (MUF-N) and MUF-phosphate disodium salt (MUF-P) were used as model substrates for β-glucosidase, β-N-acetylg glucosaminidase (NAGs) and phosphatase, respectively (Kang and Freeman 1999). The copy numbers of bacterial 16S ribosomal RNA (16S rRNA) genes were measured to estimate the bacterial abundance in the soil. DNA was isolated by using the UltraClean Soil DNA Isolation Kit (MoBio Laboratories, USA) on 1 g of the frozen soil sample.

A total of 16 Landsat 7 (L7) Enhanced Thematic Mapper plus and Landsat 8 (L8) Operational Land Imager satellite data were used to estimate the changes in water surface areas over the reservoir from July 2013 to August 2015. Both types of data were atmospherically corrected by an image analysis software (ENVI, Exelis Visual Information Solutions), which allows fast line-of-sight atmospheric analysis of hypercubes algorithm to produce reflectance. To identify water areas, Otsu’s method was applied, which is a commonly used image threshold-based segmentation approach based on the assumption of a bi-modal histogram with two classes (i.e., water versus non-water) (Li et al 2013, Du et al 2014, Rokni et al 2014).

3. Results and discussion

3.1. Drought effects on reservoir water level and surface area

The summer precipitation from June through August was very low at 369 mm in 2014 and 457 mm in 2015, although the summer precipitation averaged 786 mm over the previous four decades from 1968 to 2007, accounting for about 60% of the average annual precipitation of 1300 mm (Park et al 2010). The annual precipitation in 2014 and 2015 represents the two lowest annual precipitation records since the dam construction in 1973 (figure 2). The unusually low summer and annual precipitation over two consecutive years appear incongruent with the recent trends and future predictions of precipitation in Northeast Asia (Choi et al 2009, Hijioka et al 2014). Increases in summer precipitation and the frequency and intensity of heavy precipitation events have been observed in some parts of East Asia including the Lake Soyang watershed (Choi et al 2009, Park et al 2010). The fifth IPCC report assessed that future increases in precipitation extremes related to the monsoon climate would be highly likely in East Asia (Hijioka et al 2014).

The unusually low precipitation in the last two years resulted in gradual decreases in the reservoir water level from the previous peak of 190 m in July 2013 to the record level of 152 m on the sampling day of 22 June 2015 (figure 2). An ‘emergency’ status, as defined based on a critical level of reservoir water storage by the Water Management Information System of...
Korea, lasted for 151 d in 2015, accounting for 41% of the total number of days such designated since 1985. As a result, the reservoir surface area observed by satellite remote sensing decreased from 38.2 km² in July 2013 to 22.9 km² in June 2015 (figures 2, S1). A comparison of the reservoir surface area between the two dates revealed an exposed area of 15.3 km² along the reservoir margins.

3.2. Field CO₂ efflux measurements

The pCO₂ in the reservoir surface water averaged 211 μatm over the two-week monitoring period and was constantly lower than the mean atmospheric pCO₂ of 424 μatm measured at a downstream river site (figure 3). Diurnal fluctuations in pCO₂ generally concurred with day-to-night shifts in light intensity. Day-to-day changes in pCO₂ generally corresponded to variations in temperature, as indicated by a significant positive relationship between daily means of water temperature and pCO₂ ($r^2 = 0.594$, $P = 0.002$). The concurrent changes in water temperature and pCO₂ suggest that daily variability of pCO₂ is strongly coupled to day–night cycles of metabolic activity, while wind forcing can also play a crucial role in air–water CO₂ exchange and temporary partial mixing leading to increases in surfical water pCO₂ at longer timescales such as the biweekly scale (Morales-Pineda et al. 2014).

The fluxes of CO₂ between the reservoir and the atmosphere calculated from the measured values of pCO₂ indicated a small sink of atmospheric CO₂ in the reservoir water body, averaging at 139.8 mg C m⁻² d⁻¹ during the 2-week monitoring period (figure 4). In a 5 year eddy covariance flux monitoring at a boreal lake
in Finland, Huotari et al (2011) also observed a small sink of CO₂ during summer months and attributed it to the seasonal increase in the lake primary production. The observed level of CO₂ flux represents the lowest end of the wide CO₂ flux range reported for 85 hydroelectric reservoirs worldwide (figure 4 insets; Barros et al 2011). In contrast to many reservoirs functioning as a source of CO₂ globally, the observed small sink might reflect the relatively old age of the reservoir and its northern location, which have been suggested as the two most important factors linked to low C emissions from hydroelectric reservoir (Barros et al 2011). Considering the rapid declines in GHG emissions within years following the initial peaks associated with the decomposition of flooded vegetation and soil organic matter during the initial flooding phase (Abril et al 2005, Teodoru et al 2010), the old reservoir that was built in 1973 might release or absorb relatively small amounts of CO₂ depending on season. Further measurements of pCO₂ in other times than the monitored period, together with measurements of CH₄ concentrations and fluxes, are required to provide a more complete assessment of the role of the studied reservoir as a C sink or source.

Chamber measurements of CO₂ efflux exhibited large spatial variations along the transect spanning from the inflowing water through the recently exposed sediments to the vegetated areas (figure 4). CO₂ efflux rates were higher in the recently exposed sediments than in the drier vegetated sediments. Gravimetric soil water content on a dry soil basis was on average 66% for the vegetated sediments and 82% for the recently exposed sediments. CO₂ efflux was only slightly positive over the flooded sediment along the margin of the sediment bank, whereas very large CO₂ effluxes were measured over the rapidly flowing water 80 cm from the sediment bank. The extremely large CO₂ efflux compared to the small water sink of CO₂ observed near the dam and the small flux of CO₂ released from the adjacent stagnant water along the edge of the sediment bank indicate a potential enhancement of C efflux by the turbulent water.

The very high rates of CO₂ efflux observed for the recently exposed sediments 0–100 m from the shore exceeded the rates measured for dried watercourses in a Mediterranean river during a summer drought period (von Schiller et al 2014) and rewetted streambeds of ephemeral waterways in Arizona (Gallo et al 2014). When von Schiller et al (2014) considered the enhanced CO₂ efflux from dried watercourses, the estimate of CO₂ emission from the studied watershed increased by 0.6%–15%.

3.3. Production potentials of CO₂, CH₄ and N₂O
Changes in gas concentrations in the headspace during 48 h laboratory incubation of surficial sediments provided estimates for the potential production or consumption of three GHGs (figure 5). In agreement with field chamber measurements of CO₂ efflux, the rate of CO₂ production was significantly higher in the recently exposed sediments 0–100 m from the shore than that of the flooded sediments and the vegetated sediments. The relatively low rates of CO₂ production in the flooded sediments underlying the rapidly flowing water support the suggestion that the unusually large CO₂ effluxes observed in the field might have resulted from turbulence-enhanced increases in CO₂ evasion from the flowing water rather than from the bottom sediment. The lack of mixing in the stagnant water of the incubation bottles might have reduced the water–air gas exchange considerably. The rates of CO₂ production in the recently exposed sediments were even higher than the rates of organic C mineralization determined for sediments collected...
across a continuum from the inflow to a tropical hydroelectric reservoir in Brazil (Cardoso et al 2013).

The production of CH₄ and N₂O was also significantly higher in the recently exposed sediments than in the other sediments. The negative values of CH₄ production indicated the role of the vegetated sediments as a sink, whereas the recently exposed sediments exhibited relative low, but significantly higher rates of CH₄ production than in the other sediments. The fact that the production of three GHGs increased as a consequence of enhanced O₂ availability in the recently exposed sediments may seem inconsistent with the usual contrasting effects of enhanced aeration on aerobic and anaerobic processes involved in the production of GHGs. However, high respiration rates might concur with anaerobic processes producing CH₄ and N₂O in some localized anaerobic microsites (Gallo et al 2014). An alternative explanation for the enhanced potentials of CH₄ production might be oxic CH₄ production mechanisms such as abiotic CH₄ formation under oxic conditions (Jugold et al 2012). The increased gas production in the recently exposed sediments relative to other locations was more pronounced for N₂O than for CH₄, implying that N₂O may also be derived from aerobic processes such as nitrification (Gallo et al 2014).

3.4. Drought effects on sediment microbial activity
Spatial variations in enzyme activity were generally in line with the CO₂ efflux measurements and GHG production potentials (figure 6). Although enzyme activity was highest in the two recently exposed sediments, spatial differences were more pronounced for N₂O production than for CH₄, implying that CH₄ may also be derived from aerobic processes such as nitrification (Gallo et al 2014).

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Figure 5. Rates of potential production of CO₂ (mg C m⁻² d⁻¹), CH₄ (μg C m⁻² d⁻¹) and N₂O (μg N m⁻² d⁻¹) from sediments during 48 h incubation at 20 °C. The different letters next to symbols indicate significant differences in means at P < 0.05. Tukey HSD was used for post hoc ANOVA testing.

Figure 6. Enzyme activities (nmol diqc g⁻¹ dry soil min⁻¹) of phenol oxidase and three hydrolases (β-glucosidase, phosphadase and N-acetyl-glucosamidase) in flooded bottom sediments A and B and exposed sediments (C–F). The different letters above the bars indicate significant differences in means at P < 0.05. Tukey HSD was used for post hoc ANOVA testing.
Freeman (2011) combined in situ manipulations, laboratory incubations and field observations to show that increased O₂ availability during droughts substantially enhances phenol oxidase activity in peats, causing a cascade of biogeochemical reactions including a reduction in phenolic compounds and a subsequent boost in microbial breakdown of organic matter.

Anoxia often prevails in hypolimnia and lake bottom sediments, creating unfavorable conditions for the decomposition of allochthonous organic matter that usually has more recalcitrant components and is buried in anoxic sediments more efficiently than autochthonous compounds (Bastviken et al 2004, Sobek et al 2009, Tranvik et al 2009). In the majority of lake sediments, anoxic conditions prevail below the thin uppermost layer that typically a few mm, so C burial efficiency in these anoxic sediments is primarily controlled by oxygen exposure time (Sobek et al 2009). In contrast, the organic matter stored in very old sediments can be readily degraded by aerobic bacteria under oxic conditions (Moodley et al 2005). The availability of O₂ might have expanded from the usually very thin (a few mm) gas-permeable layer to several or tens of centimeters in the surficial layers of the sediments >1 m thick exposed along the reservoir margins to release phenol oxidases from inactivation, accelerating the degradation of phenolic compounds. Since our enzyme measurements were conducted with bulk samples from the top 5 cm surficial sediment, the results cannot distinguish vertical differences in O₂ availability and enzyme activity across the top layer and underlying deeper sediments. Although complete desiccation might decrease enzyme activity (Pohlon et al 2013), higher moisture levels in the recent sediments C and D than at E and F might have sustained the activity of extracellular enzymes above the desiccation threshold that would shift microbial community composition and lower enzyme activity. Enzymes β-glucosidase and N-acetylglucosaminidase generally followed the pattern of phenol oxidase. However, a slightly different pattern of phosphatase appears to be related to the different sources of the enzyme. Unlike bacteria-derived enzymes, the contribution of phosphatase from algae and plants can be substantial in sediments with plant cover (Rengefors et al 2001).

The activation of enzymes appears to be related to increases in microbial abundance, as suggested by the greater gene copy numbers of bacteria in the exposed sediments than in the flooded sediments (figure 7). However, this was not accompanied by a shift in the microbial community structure. Bacterial, archaeal and fungal community structures of the flooded sediments at points A and B were clearly distinguished from those of the exposed sediments at points C–F, whereas those of the recently exposed sediments at points C and D did not differ substantially from the vegetated sediments at points E and F (figure S2).

Increased 16S rRNA gene copy numbers (figure 7) and similar microbial community compositions across the exposed sediments (figure S2) suggest that the microbial community structure does not respond rapidly to water level fluctuation, but may be confined by other characteristics such as soil texture or organic matter content. The overall results suggest that enhanced aeration in sediments during extended droughts might promptly increase microbial abundance and activity with no apparent shifts in the microbial community composition. The lack or delay of the response of microbial community structure to altered moisture regimens has been observed in drying or rewetted river sediments (Amalfitano et al 2008, Pohlon et al 2013). Physiological adjustments or resilience of the microbial community might delay the structural rearrangement in response to temporary changes in moisture and aeration.
4. Implications and future research needs

The role of lakes and reservoirs as an important modifier of the C transport from the continents to the oceans has been attributed to efficient C burial in sediments in which the mineralization of large inputs of allochthonous organic matter is often limited by oxygen availability (Sobek et al 2009) and temperature (Gudasz et al 2010, Marotta et al 2014). Globally, the sediments of lakes and reservoirs can store up to 820 Pg C, and the annual increment of organic C burial in these sediments at the rate of 0.2–0.6 Pg C yr\(^{-1}\) exceeds that of the ocean sediments by a factor of three (Cole et al 2007, Tranvik et al 2009, Ciais et al 2013). The long-term average of annual C burial in natural lakes is 4.5–14 g C m\(^{-2}\) yr\(^{-1}\) (Tranvik et al 2009). The mean daily CO\(_2\) efflux measured at the four sediment locations (6.3 g C m\(^{-2}\) d\(^{-1}\); figure 4) amounts to the annual C burial in natural lakes. If the average CO\(_2\) efflux measured at the four locations persisted for 151 d in the ‘emergency’ status, the cumulative C release from the exposed sediments (951 g C m\(^{-2}\)) could have approached or exceeded the high annual C burial in the sediments of eutrophic impoundments (Downing et al 2008).

The combined results from the field measurements of reservoir pCO\(_2\) and sediment CO\(_2\) effuxes, sediment microbial activity measurements and remote sensing of changes in the reservoir surface area during an extreme drought event suggest that drought-induced temporary activation of microbial organic matter processing can drastically increase the release of CO\(_2\), CH\(_4\) and N\(_2\)O from exposed sediments. Despite the short study period and limited replications of the field transect measurement, this study provided rare insights into the potential effects of extreme droughts on the C balance of hydroelectric reservoirs. Although many studies have explored the potential effects of climatic warming on lake C balance (Tranvik et al 2009, Gudasz et al 2010, Marotta et al 2014), no direct measurements of altered rates of GHG emissions from drought-affected sediments of hydroelectric reservoirs have been reported. Extreme climate events are projected to occur more frequently in a changing climate, affecting the C balances of diverse terrestrial and aquatic ecosystems (Reichstein et al 2013). Large pulses of GHGs observed in this study emphasize the importance of stochastic C losses during extreme droughts in the C balance of hydroelectric reservoirs that store increasing amounts of C in sediments over time (Barros et al 2011). However, our exploratory research could not address complex interactions between area changes, temperature and humidity that might differ greatly across different timescales. GHG emissions from both the exposed and buried sediments can be more strongly influenced by temperature changes than by area or humidity changes (Gudasz et al 2010, Marotta et al 2014).

Although we observed a temporary boost in microbial organic matter degradation in drying sediments, a longer-term observation might have shown that the temporary activation can shift to a downturn of microbial activity after passing a desiccation threshold. Future study should systematically examine stepwise changes in environmental conditions and microbial metabolism in drying sediments of different depths from the initiation of a drought through desiccation to rewetting.

Similar to the Lake Soyang, many global reservoirs created by flooding of a main river and tributary valleys have branching arms and indented shoreline. Although the Lake Soyang is deep along the main branch near the dam, many branching arms receiving inflowing streams or rivers have a rather convex basin hypsometry. Compared to a deeper and more concave basin, larger areas of sediment surface in the convex basin can be exposed to small changes in the water level during droughts, resulting in dramatic alterations of sediment metabolic activity and organic matter degradation. Although care should be exercised in extrapolating temporary increases in C losses from the exposed sediment shown in this case study to global reservoirs, it is evident that the C balance of hydroelectric reservoirs can be easily disrupted by sensitive responses of sediment exposure and organic matter degradation during droughts. C losses resulting from enhanced C emissions from dried waterways during extended droughts must be considered in future assessments of the C balance of hydroelectric reservoirs.

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