


Effects of river damming on biogenic silica turnover: implications for biogeochemical carbon and nutrient cycles

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Received: 13 January 2017/Revised: 1 March 2017/Accepted: 24 March 2017/Published online: 30 March 2017
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Abstract Rivers link terrestrial ecosystems and marine ecosystems, and they transport large amounts of substances into oceans each year, including several forms of silicon (Si), carbon (C), and other nutrients. However, river damming affects the water flow and biogeochemical cycles of Si, C, and other nutrients through biogeochemical interacting processes. In this review, we first summarize the current understanding of the effects of river damming on the processes of biogeochemical Si cycle, especially the source, composition, and recycling process of biogenic silica (BSi). Then, we introduce dam impacts on the cycles of C and some other nutrients. Dissolved silicon in rivers is mainly released from phytolith dissolution and silicate weathering. BSi in suspended matter or sediments in most rivers mainly consists of phytoliths and mainly originates from soil erosion. However, diatom growth and deposition in many reservoirs formed by river interception may significantly increase the contribution of diatom Si to total BSi, and thus significantly influence the biogeochemical Si, C, and nutrient cycles. Yet the turnover of phytoliths and diatoms in different rivers formed by river damming is still poorly quantified. Thus, they should be further investigated to enhance our understanding about the effects of river damming on global biogeochemical Si, C and nutrient cycles.

Keywords River damming · Biogenic silica · Biogeochemical cycles · River ecosystem

1 Introduction

Rivers are the main way for the ocean to receive terrestrial matters. They play a significant role in the geochemical and biogeochemical cycles of silicon (Si), carbon (C), and nutrients (Ver et al. 1999). Dissolved substances and particulate matter transported through rivers account for 90% of the fluxes from land to coastal zones (Liu et al. 2009). Globally, about two-thirds of rivers are intercepted by approximately 40,000 large dams (a height exceeding 15 m) and by more than 800,000 small dams (Nilsson and Berggren 2000). They provide various social service functions such as hydropower production and flood control. However, anthropogenic perturbations of water courses have influenced material transport through aquatic ecosystems including rivers, streams, reservoirs, lakes and estuaries. It thus affects substance globally biogeochemical cycles (Aumont et al. 2001; Regnier et al. 2013).

Damming in river systems does not only increase the residence time and temperature of the reservoir water, but it also decreases the functions of loaded material stratifications, water turbulence modification, and the particulate matter content (Klaver et al. 2007). It therefore promotes autochthonous primary productivity (Friedl and Wüest 2002). Depending on the water discharge, which varies from 1850 to 12,000 m³·s⁻¹, the average velocity can vary from 0.2 to 1.65 m·s⁻¹ at the terminal of the Iron Gate I Reservoir on the Danube River and 0.1 to 0.60 m·s⁻¹ at the front of the Iron Gate I Dam (Bocaniov 2002; McGinnis et al. 2006). Generally, much of upstream water carrying materials are intercepted in the reservoir, affecting the

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original material flow processes (Syvitski et al. 2005). When the reservoir water level reaches flood discharge line or electric power production is needed, the floodgate is opened, which could make lots of reservoir water and its carrying materials flow to downstream regions (Humborg et al. 2002). In the short term (discharge to a certain boundary will close the valve), the drainage process could increase material input flux of downstream water. Compared with dry season, the exchange frequency of retaining water and drainage process is higher in rainy season. Additionally, the construction of dams widely exists on global scale (Aumont et al. 2001; Regnier et al. 2013). Therefore, river damming could have a seasonal and non-seasonal effect on the global biogeochemical cycles of loaded elements (Friedl and Wüest 2002; Humborg et al. 2002), the dynamic features of water and the water quality of downstream rivers (Burford et al. 2011).

Si is the second most abundant element in the Earth's crust (Wedepohl 1995; Conley 2002). The Si cycle is closely related to the cycles of C and other nutrients in aquatic ecosystems (Hudson et al. 1999; Ge et al. 2015). However, Si is a key limiting element in aquatic ecosystems because it is mainly fixed in the form of silicate minerals and quartz fractions that cannot be taken up by aquatic organisms (Ittekkot et al. 2000; Ge et al. 2015). Dissolved silicon (DSi), mainly originates from phytolith dissolution and silicate weathering, is a key nutrient in river and marine ecosystems (Laruelle et al. 2009). Therefore, the influence of damming activities on the variation of biogenic silica (BSi) content should be taken into account when considering the processes involved in the biogeochemical Si cycle (Conley 2002), and its impacts on other nutrients should not be neglected. Reservoirs could also act as a sink of other nutrients such as phosphorous (P) and nitrogen (N) (Josette et al. 1999; Uhlmann et al. 1995; Uhlmajnn and Horn 1992). For example, P retention varied from 16% to 98% in the Chaffrey Dam Reservoir (Australia). As for nitrogen, the sediment acted as a net sink with maximum retention of 89% or as a net source (Sherman et al. 2001).

Phytoliths are microscopic opaline structures of silica formed in some plant tissues and may be preserved in soils or sediments after plant decay (Bartoli and Wilding 1980; Kameník et al. 2013; Anala and Nambisan 2015). They are one of the most important components of river BSi (Cary et al. 2005; Ran et al. 2015; Ge et al. 2015). During the process of H_4SiO_4 polymerization in plant tissues, 0.2%–5.8% of the organic C can be wrapped into the phytoliths (Parr and Sullivan 2005, 2011; Parr et al. 2010; Zuo and Lü 2011). After plant litter decomposition, some sequestered C under the protection of the phytoliths may be preserved in soils or sediments for hundreds to thousands of years (Parr and Sullivan 2005; Blecker et al. 2006). Recently,

these C occluded within phytoliths (PhytOC) are strongly suggested to be one of the most important long-term biogeochemical C sequestration mechanisms (Parr and Sullivan 2005; Song et al. 2012, 2016a; Guo et al. 2015; Sun et al. 2015). However, a portion of the phytoliths could be exported from soils and enter into rivers through soil erosion. Thus, this process becomes an important source of river BSi (Cary et al. 2005; Cornelis et al. 2011). Therefore, the dissolution and migration of phytoliths in river ecosystems are worthy of consideration for the better understanding of Si and C cycles in terrestrial ecosystems, especially after the construction of dams.

As another important BSi fraction in aquatic ecosystems, diatoms are widely distributed in rivers, lakes, and oceans (Ahluwalia and Renuka 2016). The growth of diatoms requires a large amount of DSi to develop the siliceous cell wall or “frustule” (Nelson et al. 1995). After river damming, reservoirs become more beneficial environments for the growth of phytoplankton, including diatoms, due to eutrophication and a relatively long water residence time (Soballe and Kimmel 1987; Kawara et al. 1998). Furthermore, the hydrological alterations caused by river damming decrease the DSi loads in downstream ecosystems, which could profoundly influence the coastal zone and marine ecosystem (Conley et al. 1993; Josette et al. 1999; Humborg et al. 2000, 2002), including changes in species composition and nutrient-recycling processes.

Though many studies have reported the role of BSi in sediments and river water (Olivie-Lauquet et al. 2000; Cary et al. 2005; Ran et al. 2015; Zang et al. 2016), there is poor understanding of how to control the BSi and its coupling with the biogeochemical Si, C, and other nutrient cycles in rivers and reservoirs worldwide. In this review, we first introduce the characteristics of BSi. Then, we review phytolith dissolution and migration, and the relationship between diatoms and other nutrients. Finally, we discuss the interactions of Si, C and nutrients in aquatic ecosystems. This could not only give better understanding of Si biogeochemistry, but also help to fill up the gap on the coupling among Si, C, and other nutrient cycles.

2 Biogenic silica characteristics in rivers

Annual gross production of BSi is estimated to be $240 \text{ T mol Si year}^{-1}$ in marine ecosystems (Treguer et al. 1995), and the primary composition of BSi is diatoms, which account for 90% of the BSi (Nelson et al. 1995). However, in inland aquatic ecosystems, the contribution of phytoliths to BSi is higher than that of diatoms (Cary et al. 2005; Ran et al. 2015, 2016; Zang et al. 2016). For example, phytoliths contribute to 92.8%–98.3% of the total BSi volume in sediment samples from the Pahang River in Malaysia,

whereas the mean contributions of diatoms and sponge spicules are 3.85% and 0.22%, respectively (Table 1; Zang et al. 2016). In the Nyong Basin, approximately 90% of the BSi is derived from phytoliths, whereas diatoms and thecamoebians only account for a small fraction of BSi in the suspended matter of rivers (Table 1; Cary et al. 2005). Compared with Pahang River and the Nyong Basin, the contribution of phytoliths to the BSi in the Pontain, Endau, Yangtze and Huanghe rivers is relatively low, accounting for only 23.8%, 12.8%, 43% and 49.6%, respectively (Ran et al. 2016). These variations are likely to be due to the differences in climate, river shore topography, and river coastal biomass.

In terrestrial ecosystems, soil erosion could transport a certain amount of DSi and BSi (phytoliths) from soils to rivers. It has been reported that there is about $2.6 \times 10^6 \text{ t}\cdot\text{a}^{-1}$ of phytolith loss due to soil erosion on the Chinese Loess Plateau (Zuo et al. 2014). Some undecomposed and incompletely decomposed litters, containing a significant amount of phytoliths, can be directly washed into rivers and streams. This process can occur readily on rainy days and in areas with large slopes at water edges (Meyer and Wischmeier 1969; Cary et al. 2005). More importantly, some phytoplankton, such as diatoms in the aquatic ecosystems, takes up DSi to develop a siliceous shell during their growth process (Capellacci et al. 2013). Although siliceous sponges are widely distributed in the oceans and freshwater environments, their contribution to

BSi only accounts for 0%–7.89% (Table 1). Additionally, studies on BSi in salt marsh settlements have indicated significantly in situ deposition of plant BSi (Norris and Hackney 1999). In summary, the major sources of BSi in aquatic ecosystems are the erosional inputs from terrestrial ecosystems and production from phytoplankton (Fig. 1).

Diatoms can proliferate in a wide range of depth habitats, flow conditions and water chemistry conditions (Battarbee et al. 2002). As the lowest contributor of BSi in water, siliceous sponges flourish in deep lakes such as Baikal, Tanganyika and Taupo (De Ronde et al. 2002; Belikov et al. 2005) and are common in numerous shallow water areas. The BSi content of natural waters varies seasonally, and the contribution of diatoms to primary productivity is mainly concentrated in the late winter or early spring blooms (Brzezinski and Nelson 1995). Thus, the contribution of diatom fractions to BSi during these periods is generally higher than in other periods. Previous studies have shown that the accumulation of BSi in lake sediments varies with trophic status (Schelske et al. 1983; Conley et al. 1993; Conley and Schelske 2002). A high trophic status, especially under high Si concentrations, may result in the rapid growth of diatoms in lakes and ultimately lead to an increase in the supply of BSi from diatom fractions. In addition, the BSi content (e.g., phytoliths, in the rivers) is related to plant phytolith production in terrestrial ecosystems and soil erosion (Cary et al. 2005; Ran et al. 2015). High phytolith loads in rivers are

Table 1 Composition of biogenic silica in river sediments or suspended matter (%)

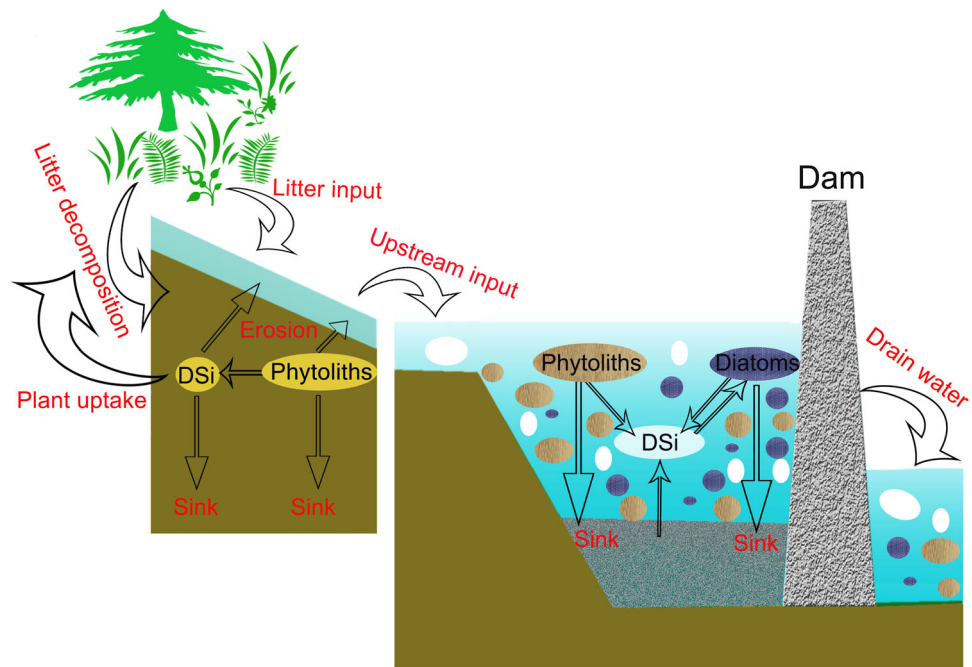
Rivers	Phytoliths	Diatoms	Sponges	Thecamoebae	References
Sediments ^a					
Pahang River St1	96.5	2.81	0.65	–	Zang et al. (2016)
Pahang River St2	96.8	3.20	0	–	Zang et al. (2016)
Pahang River St3	92.8	7.17	0	–	Zang et al. (2016)
Pahang River St4	96.1	3.62	0.33	–	Zang et al. (2016)
Pahang River St5	98.3	1.75	0	–	Zang et al. (2016)
Pahang River St6	95.1	4.53	0.32	–	Zang et al. (2016)
Pontain River	23.8	68.8	7.50	–	Zang et al. (2016)
Endau River	12.8	79.3	7.89	–	Zang et al. (2016)
Suspended matter					
Yangtze River ^b	43.0	55.0	1.90	–	Ran et al. (2016)
Yellow River ^b	49.6	50.6	0.13	–	Ran et al. (2016)
Mengong ^c Outlet	93	3	–	4	Cary et al. (2005)
Messam ^c (Awout)	89	8	–	3	Cary et al. (2005)
Pont-Soo ^c (Soo)	99	0	–	1	Cary et al. (2005)
Mbalmayo ^c (Nyong)	91	5	–	4	Cary et al. (2005)
Olama ^c (Nyong)	94	1	–	5	Cary et al. (2005)

^a The data is detected in May, and counted in frequency

^b The date is an average value in a year, and counted in frequency

^c The data is counted in mass percentage from Nyong basin

Fig. 1 The migration of phytoliths from land to aquatic ecosystem and cycle of BSi in the reservoir



found in areas where plants are highly productive such as the forest and grassland cover of inter-tropical low elevation areas (Lucas and Nahon 1993; Runge 1999; Wüst and Bustin 2003). Furthermore, many of the phytoliths and diatom fragments are buried in river sediments (Zang et al. 2016).

The BSi dissolution rates are highly variable with the decrease of water depth, and the natural BSi dissolution could be significantly accelerated in silica-depleted surface waters on the basis of the nonlinear kinetics (Rickert et al. 2002). Previous studies have shown that the dissolution of BSi had a significant sensitivity to temperature variations (Rickert 2000; Van Cappellen et al. 2002). Therefore, current global warming is likely to have an impact on the solubility of BSi in waters (Laruelle et al. 2009; Bernard et al. 2010).

Recycling of BSi is the main source of DSi needed to provide phytoplankton blooms in natural waters, especially for the diatoms (Parker et al. 1977). After the death of diatoms in rivers or reservoirs, the vast majority of diatoms will be dissolved in the water column and only a small fraction of them can therefore be buried (Van Cappellen et al. 2002). While there are regional differences in the dissolution of BSi, the ratio of the diatom dissolution rate to the diatom formation rate in surface waters does not show any significant variation with latitude (DeMaster et al. 1991; Nelson et al. 1996). For example, Rickert et al. (2002) have showed that BSi from the Norwegian Sea is approximately 10 times more soluble than from the Southern Ocean, which reflected differences in species-specific diatom dissolution rates.

3 Dissolution and migration of phytoliths in intercepted rivers

3.1 Phytolith dissolution

Some of phytoliths enter soils (Hart and Humphreys 2004), while others are transported into rivers or streams through soil erosion (Cary et al. 2005; Ran et al. 2015, 2016). Phytolith dissolution is affected by several factors, such as the specific surface area of phytoliths, environmental temperature (i.e. fire), pH, salinity, ionic strength, plant organ and plant cultivars, as well as the disturbance of waters (Frayssé et al. 2006; Li et al. 2014; Ngoc Nguyen et al. 2014; Cabanes and Shahack-Gross 2015; Unzué-Belmonte et al. 2016). For example, Frayssé et al. (2006) demonstrated that bamboo phytoliths had the lowest solubility at pH \sim 3, which may explain why phytoliths are well preserved in the acidic soil horizons of Réunion Island. In addition, Ngoc Nguyen et al. (2014) have shown that the phytolith dissolution rate declined in the presence of cations such as aluminum ions. Through microscope observations, Zang et al. (2016) found that phytoliths were corroded in sediment samples. This finding highlights that a portion of phytoliths could be dissolved, further offering a source of DSi in river waters.

3.2 The migration of phytoliths

During the growth of hydrophytes and terrestrial plants, DSi is taken up by plant roots and deposited as BSi (phytoliths) in plant tissues (Conley 2002). When the litter

produced during the life cycle of plants undergoes decomposition, the phytoliths are released directly into soils (Mulholland and Rapp Jr 1992; Li et al. 2013). Song et al. (2016b) estimated that the soil surface stable BSi content (mainly phytoliths) of litter input may reach 70%–90% at a centennial scale. This implies that 10%–30% of soil phytoliths could be dissolved or transported to the rivers due to soil and litter erosion at a centennial scale (Cary et al. 2005; Ran et al. 2015). In the transfer process along rivers, some phytoliths may be dissolved in water, while the rest of them may accumulate in the water columns or sediments (Fig. 1).

In aquatic ecosystems, phytoliths tend to be dissolved in situ or in the process of migration. In recent decades, the reduction in river DSi transported to the coastal regions after dam constructions has been increasingly realized (Humborg et al. 2000). For instance, the increase in the number of dams and impoundments along rivers has drastically altered the delivery of DSi and BSi (especially for phytoliths) flowing from land to ocean since the 1950s (Conley 2002; Humborg et al. 2006). In addition, the study of Derry et al. (2005) showed that most of the silica in Hawaiian streams originates from the BSi pool, whereas, only a small fraction of river Si originates from direct mineral–water reactions according to the germanium/Si ratios. Thus, the dissolution of phytoliths during migration process is important for the understanding of the biogeochemical Si cycle mechanism.

After the dam constructions, reservoirs will retain abundant phytoliths and DSi, as well as other nutrient materials due to the reduction of flow rates and the increase of water residence time (Conley et al. 2000; Friedl and Wüest 2002). Subsequently, the growth and reproduction of diatom within reservoirs could rapidly increase because of sufficient Si supply. Although drainage process can release a certain amount of DSi and BSi (diatom and suspended phytoith particles) to downstream regions, massive DSi and BSi have been intercepted and deposited into reservoir sediments (Conley 2002; Friedl and Wüest 2002). Therefore, dams could drastically affect the delivery of DSi and BSi, especially for phytolith particles, through rivers (Humborg et al. 2006).

4 Phytoplankton versus nutrients in reservoirs

4.1 The relations between phytoplankton and nutrients

Phytoplankton are widely distributed in aquatic ecosystems and are an important primary producer in natural waters where they are a food item for many aquatic animals. Their growth and reproduction are affected not only by

disturbances of the water column, but also by the content of various nutrients in the water (Madhu et al. 2007). Many studies have found that increasing nitrogen (N) and phosphorus (P) concentrations in the water from anthropological activities can trigger water eutrophication (Ryther and Dunstan 1971; Conley et al. 2009; Dodds and Smith 2016). However, the growth of some phytoplankton, especially diatoms, depends on the supply of DSi. Thus, the concentration of DSi can affect the species composition of phytoplankton in aquatic ecosystems (Ittekkot et al. 2000). For example, diatoms mainly take up DSi during their growth and the precipitation flux of phytoplankton is controlled by DSi (Conley and Malone. 1992; Laruelle et al. 2009). Malone et al. (1991) reported that low DSi concentrations would lead to a rapid decrease of phytoplankton biomass and a change from diatom-dominated communities to other phytoplankton.

Reservoirs can retain a large amount of river water and have a significant influence on Si transport after damming (Mayer and Gloss 1980; Conley et al. 1993, 2000). The reduction of the Si output to the oceans will alter the ratio of nutrients utilized by phytoplankton and affect the entire food web in aquatic ecosystems (Turner et al. 1998; Humborg et al. 2000). High N/Si or P/Si ratios due to a decline in the Si content and/or an increase in the N and P content, favor the growth of non-siliceous algae, while low ratios are beneficial to the growth of diatoms (Shanthi et al. 2014). Different inputs of nutrients have led to a significant increase in the frequency of phytoplankton bloom since the 1970s (Table 2). Additionally, the water levels of many reservoirs are significantly reduced during the dry season, and this process is associated with an increase in suspended solids (Dejenie et al. 2008). Many studies have reported a positive correlation between the phytoplankton biomass and total P concentration in water (Dejenie et al. 2008; Rangel et al. 2012). High P/Si or N/Si ratios have adverse effects on the river ecosystem (Friedl and Wüest 2002). For example, high N/Si ratios show that N is excessive with respect to the need of diatoms. The value (1) of the N/Si ratio can be regarded as a critical value (Redfield 1963; Turner and Rabalais 1991). If the N/Si ratio is higher than 1, non-siliceous algae growth will be significantly promoted. However, if it is lower than 1, non-siliceous algae growth will be limited, and diatom growth can be enhanced (Turner and Rabalais 1991). Additionally, diatoms are also sensitive to the increase of P/Si ratios (Friedl and Wüest 2002). The diatom growth could be inhibited by limited DSi concentration in water columns.

4.2 Diatom deposition in waters after damming

As shown in Table 3, particulate matter is deposited after damming, which could increase the residence time and

Table 2 Cell densities and blooms number in two different periods

Danube river	1960–1970		1980–1990	
	Cell densities (10^6 cells L^{-1})	Blooms number	Cell densities (10^6 cells L^{-1})	Blooms number
Total diatoms	7–21	8	5–300	19
Total dinoflagellates	17–51	4	5–810	14
Total Euglenophytes*	–	–	5–108	6
Total prymnesiophytes*	–	–	220–1000	3
Total blooms		12		42

Total concentration is calculated by cell densities and blooms number of each algae in the northwestern Black Sea

* A dash represent that the organism is absent. Data are from Humborg et al. (1997)

Table 3 Basic data, and DSi influx and removal of reservoirs in the world

Latitude ^a	Reservoir name	Location	Surface area (km ²)	Mean depth (m)	Residence time (year)	DSi influx (mol·year ⁻¹)	DSi removal (%)	Trophic status	References ^b
+26.97	Dongfeng	China	19.7	52	0.1	4.56×10^8	-5.46	Oligotrophic	1
+26.9	Suofengying	China	5.7	23.5	0.016	3.99×10^8	-7.30	Mesotrophic	1
+27.3	Wujiangdu	China	47.5	48.4	0.14	5.41×10^8	22.80	Eutrophic	1
+30.8	Three Gorges	China	56	18.4	0.097	4.65×10^{10}	N/A	Eutrophic	2, 3
+44.9	St. Croix	USA	35	14	0.1	N/A	3.77	Eutrophic	4
+44.4	Pepin	USA	103	8.9	0.05	N/A	-10.80	Mesotrophic	4
+36.9	Lake Powell	USA	658	40	2.3	4.81×10^9	N/A	Oligotrophic	5, 6
+36.4	Lake Mead	USA	640	40	2.6	4.94×10^9	N/A	Mesotrophic	5, 6
+26.6	Falcon	USA	338.5	11.52	2.1	7.02×10^8	N/A	Eutrophic	5, 6
+48.3	Marne	France	48	7.2	0.46	5.39×10^7	47.00	Eutrophic	7
+48.2	Seine	France	23	7.6	0.62	5.45×10^7	57.00	Eutrophic	7, 8
+48.2	Aube	France	21	8.9	0.4	2.32×10^7	43.00	Eutrophic	7
+48.2	Amance	France	0.5	4.5	0.03	5.39×10^7	9.30	Eutrophic	7
+48.3	Champaubert	France	0.5	3.5	0.11	2.32×10^8	15.50	Eutrophic	7
+44.4	Iron Gate	Romania	156.4	17.26	0.03	1.41×10^{10}	4.00	Eutrophic	9, 10, 11
+49.2	Solina-Myszowce	Poland	24	22	0.61	3.25×10^7	20.00	Oligotrophic	12
-35.5	Lake Alexandrina	Australia	580.6	2.86	0.3	9.29×10^8	39.00	Mesotrophic	13, 14, 15

^a In the first column, “+” refers to the northern latitude and “-” refers to the southern latitude

^b References: (1) Wang et al. (2010), (2) Müller et al. (2012), (3) Ran et al. (2013), (4) Triplett et al. (2008), (5) Kelly (2001), (6) Maavara et al. (2014), (7) Josette et al. (1999), (8) Thieu et al. (2009), (9) Teodoru and Wehrli (2005), (10) Friedl et al. (2004), (11) McGinnis et al. (2006), (12) Koszelnik and Tomaszek (2008), (13) Cook et al. (2010), (14) Geddes (1984), (15) Mosley et al. (2012)

slow the rate of river transport of particulate matter. At the same time, autochthonous primary production in rivers and reservoirs is significantly promoted due to the reduction in turbidity and enhancement of light transmissivity (Domingues et al. 2014). Therefore, reservoir ecosystems could evolve from systems dominated by allochthonous organisms to ecosystems dominated by in situ production, which will alter the biogeochemical cycles of C, Si and other nutrients such as N and P in rivers (Friedl and Wüest 2002).

Si, N, and P are essential nutrients for algae in aquatic ecosystems, and an increase in their supply will stimulate

algal growth especially for diatoms (Conley 2002). Large amounts of nutrients are trapped and naturally retained in reservoirs along the aquatic continuum after river damming (Conley et al. 2000). Therefore, the transport flux of DSi to the oceans by rivers is significantly decreased (Humborg et al. 2000), whereas the DSi concentrations in the water columns of reservoirs are increased. The diatom production flux in the reservoirs will be significantly increased because the lentic environment is more favorable for phytoplankton communities after damming than lotic conditions (Okuku et al. 2016). Diatoms absorb DSi during their growth,

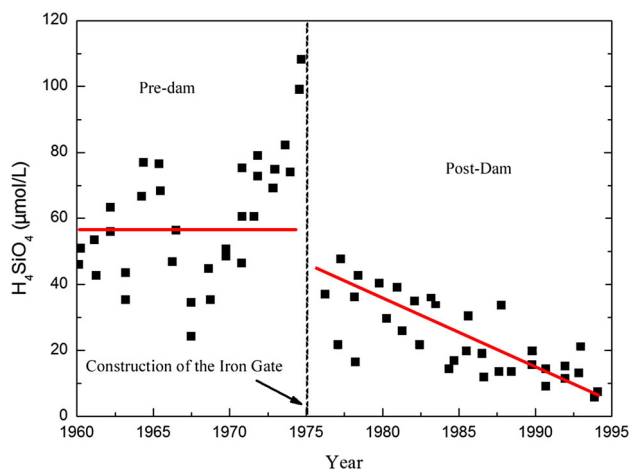


Fig. 2 Variations of DSi concentration in the Black Sea (offshore the Danube Delta) from 1960 to 1992 in winter. The *left solid line* represents the overall average value and the *right solid line* represents the trend of silicate concentration (modified from Cociasu et al. 1996)

which is removed as BSi from water bodies into sediments after they die (Rahm et al. 1996). Lakes and reservoirs retain a large quantity of diatom frustules in the bottom sediments (Van Bennekom and Salomons 1981), which may explain why the DSi concentration in the Black Sea reduced after construction of the Iron Gate (Fig. 2).

Lakes and reservoirs are particularly effective at trapping nutrients and the siliceous shells of diatoms (Shi et al. 2015). For example, the number of diatoms has a strong positive correlation with their sedimentation fluxes under eutrophication in Saldenbach Reservoir in Saxony (Uhlmajnn and Horn 1992). Diatoms have high growth rates, especially under conditions with a high silicate concentration, and their sinking rates are higher than for other phytoplankton populations due to reservoir eutrophication (Hildebrand et al. 2012). At the same time, the dissolution rates of dead diatoms are relatively slow (Loucaides et al. 2012). Therefore, the proportion of diatoms in BSi may be significantly increased in reservoir sediments and suspended matter after damming.

5 Biogeochemical silicon, carbon, and nutrient cycles after damming

5.1 Biogeochemical silicon and carbon cycles

Coupled C and Si biogeochemical cycles have occurred throughout geological time. Silicate weathering in terrestrial ecosystems is thought to be a promising way to create a long-term C sink (Brady and Carroll 1994). Simultaneously, silicate weathering is also an important source of reactive and particulate silica in rivers, and about 80% of

the net inputs are transported to the oceans by rivers (Treguer et al. 1995). However, river damming affects the transportation fluxes of reactive silica from reservoirs to downstream rivers as well as to coastal regions (Fig. 2), and subsequently has a significant impact on the phytoplankton community in rivers, reservoirs, estuaries and coastal areas.

The main sources of organic C in aquatic ecosystems are drainage systems into rivers, direct organic C inputs from adjacent terrestrial ecosystems, and C fixation of riverine organisms (Schlesinger and Melack 1981). Conley et al. (2000) reported that the DSi output fluxes had an exponential relationship with lake or reservoir areas and that the DSi concentration in lakes or reservoirs would decrease because diatom growth and deposition may deplete much of the DSi. Additionally, based on the sediment accumulation rate in the Iron Gate Dam Reservoir and the average concentration of BSi in suspended matter, Friedl et al. (2004) estimated that more than 500,000 t of BSi were retained in the reservoir each year. The process by which the concentration of DSi is reduced in reservoirs is accompanied by an increase in primary productivity, indicating that rivers after damming could produce more organic C.

5.2 Biogeochemical cycles of nutrients

Many studies have shown that reservoirs are sinks of N and P (Uhlmajnn and Horn 1992; Uhlmann et al. 1995; Josette et al. 1999). Reservoir and lake water loses N and P along with suspended solids during the deposition process (Beusen et al. 2016). The buried nutrients can be partly recycled in rivers or reservoirs. Increasing the transport of nutrients to the sediments will result in a higher net burial flux (Aller et al. 1996).

The storage of nutrients in reservoirs depends mainly on the hydrodynamics and upstream nutrient inputs, and it has a significant difference among various years (Sherman et al. 2001; Beusen et al. 2016). For example, Sherman et al. (2001) found that the retention of P varied from 16% to 98% in Chaffrey Dam Reservoir in Australia. When compared with the upstream of the Corrents River in Brazil, the reservoirs in the Corrents River have a significantly low turbidity. Furthermore, the concentrations and average percentage reduction of total P and nitrate are significantly different from the reservoirs in the upstream of the Corrents River (Fantin-Cruz et al. 2016). Although nutrients such as N and P can be trapped in reservoirs after damming, the amount of N and P discharged into the downstream by human activities exceeds the amount retained in reservoirs, which is not the case for Si (Ittekkot et al. 2000). The increases in N and P concentrations will

enhance the eutrophication frequency and result in the degeneration of coastal areas (Friedl and Wüest 2002).

5.3 Coupling of silicon and other nutrients

Artificial reservoirs have similar characteristics to rivers and lakes (Molozzi et al. 2013). Dam construction has a significant impact on material cycles through rivers because the reservoirs can trap large amounts of DSi, BSi, and other nutrients (Conley et al. 2000; Humborg et al. 2006). For example, the DSi concentration fell approximately $200 \mu\text{mol}\cdot\text{L}^{-1}$ in the Nile Estuary after construction of the Aswan High Dam (Wahby and Bishara 1980). In addition, there was a negative correlation between the DSi concentration and live storage in the reservoirs (Fig. 3; Humborg et al. 2002).

Because diatom production can be altered by changes in the molar ratios of the environmental nutrient concentrations in waters, the ratios of DSi to dissolved inorganic nitrogen (DIN) and dissolved inorganic phosphorus (DIP) could have a significant importance on diatom production (Howarth 1988). According to Redfield (1963), the potential DSi limits can be determined from the ratio of DSi:DIN ($\text{DSi:DIN} < 1$) and the ratio of DSi:DIP ($\text{DSi:DIP} < 16$). The alteration of Si:N:P ratios may shift the phytoplankton structure (Admiraal et al. 1990; Turner and Rabalais 1994). For example, the cell densities and species abundances in the surface waters of the Black Sea were found to increase when the average DSi concentrations decreased from 55 to $20 \mu\text{mol}\cdot\text{L}^{-1}$ after construction of the Iron Gate, which caused a change in the Si:N:P ratios (Fig. 2; Table 2; Cociasu et al. 1996). Although diatom blooms in the northwestern Black Sea have only increased by about 2.5 times from the 1960s to the 1980s, the number

of non-diatom (such as euglenophytes and prymnesiophytes) blooms has increased by about six times (Table 2). The reason for the phytoplankton community shift is the relative shortage of Si due to the impounding of the Iron Gate Dam. Therefore, a large portion of the N that should have been absorbed by the diatoms would be removed by the non-diatoms and ultimately promote the growth of non-diatoms (Humborg et al. 1997).

6 Conclusions and perspectives

The BSi in most rivers mainly originates from phytoliths, which are derived from the erosion of surface soils and inputs of plant litter. The dissolution and migration of BSi are important parts of the biogeochemical Si cycle and have significant implications for C and nutrient cycles. The construction of dams has a significant influence on the growth of diatoms in reservoirs and rivers, which has a substantial effect on BSi, C, and nutrient cycles. Therefore, river damming could alter the balance of Si and affect the biogeochemical cycles of C, N and other nutrients through their coupling with Si. Future studies should investigate:

- (1) The seasonal variations of the BSi composition of reservoirs with a different trophic status, and water residence time should be quantitatively studied.
- (2) Quantitative studies of the contribution of BSi, especially for phytoliths, to DSi in water columns are particularly significant, and they will provide a new perspective on the biogeochemical cycles of Si, C, and nutrients in natural waters after river damming.
- (3) A comparison of the differences in BSi composition in front of and behind the dam is needed to improve our understanding of the effects of damming on BSi translocation.

Acknowledgements We acknowledge the support from the State's Key Project of Research and Development Plan of China (2016YFA0601002) and the National Natural Science Foundation of China (41522207, 41571130042).

Compliance with ethical standards

Conflict of interest We declare no conflict of interest.

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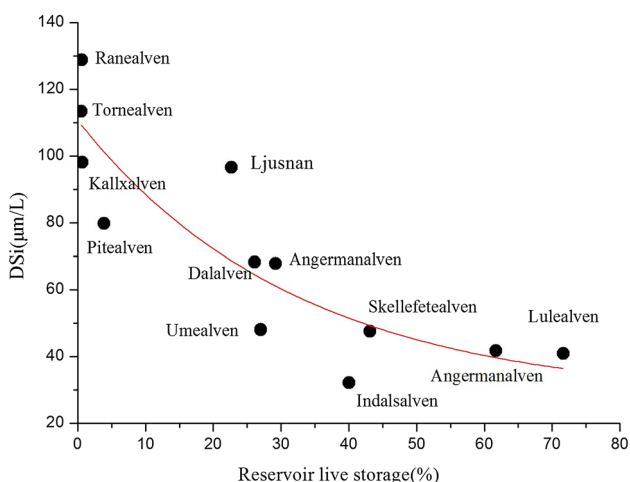


Fig. 3 Correlation between the reservoir live storage and dissolved Si concentration (modified from Humborg et al. 2002)

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