Reports

Ground Water as a Silica Source for Diatom Production in a Precipitation-Dominated Lake

Abstract. *The short-term, seasonal input of ground water to a small, precipitation-dominated oligotrophic lake in northern Wisconsin amounts to less than 10 percent of the annual water budget of the lake but accounts for nearly all the external silica loading. Silica is a necessary nutrient for diatoms. A large spring diatom bloom occurs coincident with high silica inputs from ground water when other possible silica sources are low. The mass budgets of ground water and silica in the lake system demonstrate the importance of ground-water solute inputs to the lake.*

Nutrient supply to the euphotic zone of lakes is an important factor regulating phytoplankton growth. Phytoplankton blooms have been thought to result from lake mixing (overturn), which transfers nutrient-enriched bottom waters to the photic zone, and from the addition of nutrients from streams during periods of high flow (*1, 2*). Although ground water can be a potential nutrient source, it is often ignored in lake nutrient budgets (*3*). We demonstrate here that, in lakes fed mainly by rainfall, ground water can be a major nutrient source for phytoplankton.

Lakes in temperate latitudes usually produce a large spring diatom bloom and a subsidiary fall bloom (*2*). For diatoms, silicon is a key element (*1, 4, 5*). We investigated the effect of a relatively small ground-water influent in the regulation of silica supply and diatom growth in Crystal Lake, a small (36 ha; 3.8×10^6 m^3), oligotrophic lake that does not receive stream flow or surface runoff. The lake, located in the Northern Highlands Lake District of north-central Wisconsin, contains low concentrations of dissolved constituents (alkalinity, 0.025 meq $liter^{-1}$; conductivity, 13 μS cm^{-1}; calcium, 1.2 mg $liter^{-1}$; and total dissolved phosphorus, 0.004 mg $liter^{-1}$ at spring overturn).

To determine the importance of ground water as a silica source for diatom production, we investigated the relation between changes in the biogenic silica content of the water column and the timing and magnitude of silica inputs and outputs. Changes in the silica content of the lake were determined from measurements of the forms and concentrations of silica as a function of time and depth coupled with lake bathymetry (*6*). The two forms of silica measured in the water column were dissolved reactive silica (DRS), which is directly available for biological uptake (*4*), and particulate biogenic silica (PBS), which is composed mainly of diatom frustules. Chlorophyll a concentrations were also measured (*7*). To calculate influent ground-water DRS, measurements of hydraulic conductivity, ground-water head, and DRS concentrations in a network of ground-water monitoring wells were carried out (*8*). Effluent ground-water DRS was calculated similarly, on the basis of measurements of the in-lake concentration of DRS and ground-water outflow. The gross internal loading of silica to the water column from the bottom sediments (regeneration) was calculated by mass balance on in-lake total silica (TS). Sediment traps were used to determine the gross removal of PBS from the lake water by sedimentation (*9*). Sediment cores were analyzed to determine the net permanent accumulation of PBS in bottom sediments (*10*). We also estimated the atmospheric deposition (wet and dry) of silica onto the lake (*11*).

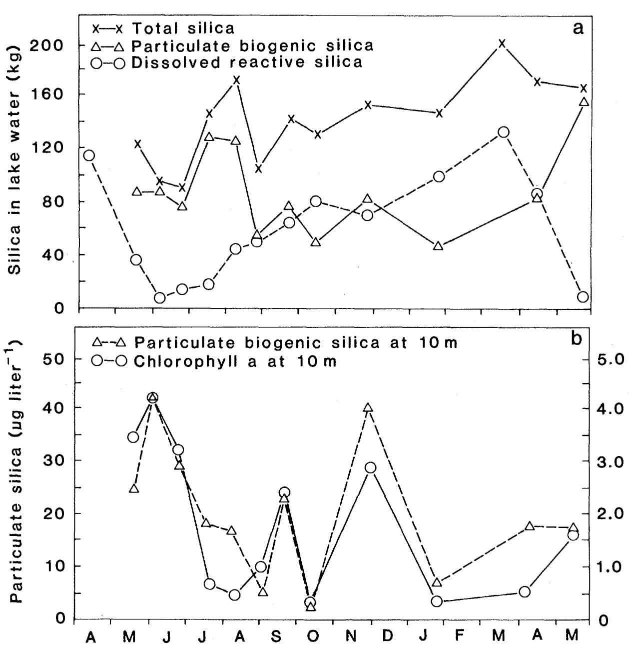


Fig. 1. Time series of silica in Crystal Lake: (a) total silica content of the lake (particulate biogenic silica plus dissolved reactive silica); (b) particulate biogenic silica and chlorophyll a concentrations at a water depth of 10 m; the close relation between the two curves shows that diatoms are a dominant phytoplankton component.

The DRS concentrations in Crystal Lake (Fig. 1a) are comparatively low (*12*). As a consequence, the lake is silica-limited and diatoms respond to silica inputs. Diatoms are a dominant phytoplankton component (Fig. 1b). The onset of diatom production at ice-out in early spring results in the rapid depletion of DRS from ~25 to <5 μg $liter^{-1}$ and a corresponding increase in diatom silica (PBS). Subsequently, PBS declines and then fluctuates at a lower level until the following spring (Fig. 1a). After depletion in the spring, the DRS content increases continually until fall overturn (Fig. 1a). During thermal stratification (June through October), an increase in the DRS content occurs in the hypolimnion, reflecting release from bottom sediments (regeneration). Transfer into the epilimnion is masked by diatom uptake. At fall overturn, DRS is transferred completely into the photic zone, and the DRS content declines slightly as a result of diatom uptake in the late fall. Subsequently, DRS increases until the onset of removal by the spring bloom.

The largest ground-water input occurs in spring (Fig. 2a), an indication that ground water is a silica source for the spring diatom bloom. However, the silica content in the water column is a function of all the various fluxes to and from the lake, and major fluxes must be compared to resolve the importance of ground water. External sources of silica are dominated by ground-water inflow (Table 1). Even though the volumetric input of precipitation is about ten times the ground-water inflow, DRS concentrations in precipitation are very low and the corresponding DRS loading from precipitation is negligible. Similarly, because concentrations of DRS are low in the lake surface water (source of effluent ground water) compared to influent ground water, the removal of DRS by ground-water outflow is small.

The only possible internal source of silica is regeneration (referring to silica released solely from bottom sediments, either through dissolution of recently deposited diatom frustules or diffusion of DRS from the pore waters of "historical" sediments). To estimate input from internal regeneration, a mass balance approach based on time-series measurements of inputs, outputs, and in-lake concentrations was used. Over a given time interval (usually 3 weeks)

$$\text{Silica regenerated from bottom sediments (gross)} = \Delta\text{TS (DRS + PBS) in lake water (net)} - \text{Input of DRS by ground water (gross)} + \text{Removal of PBS by sedimentation (gross)} \quad (1)$$

where PBS gross sedimentation (Fig. 2c) represents the flux of silica incorporated into diatom frustules in the sediment traps (*13*).

Time-series data show that ground water is a major silica source for the spring diatom bloom (Figs. 1 and 2). Ground-water input (Fig. 2a) occurs before the spring bloom (Fig. 1); hence, the DRS increase between November and March is due mainly to ground-water supplies. This input continues through June but does not produce a DRS increase after March because of concurrent removal by diatom production. Regeneration (Fig. 2b) does not become important until after the spring bloom. However, regeneration in the late summer and fall contributes to the DRS present in the spring. On an annual basis, ground water is the direct silica source for about 45 percent of the PBS sedimented (gross). Although annual regeneration probably exceeds ground-water input (Table 1 and Fig. 2), regeneration occurs during summer and fall and is important in sustaining diatom production during this period.

Silica originating in ground water is

Table 1. Silica and water fluxes in Crystal Lake (May 1982 to May 1983).

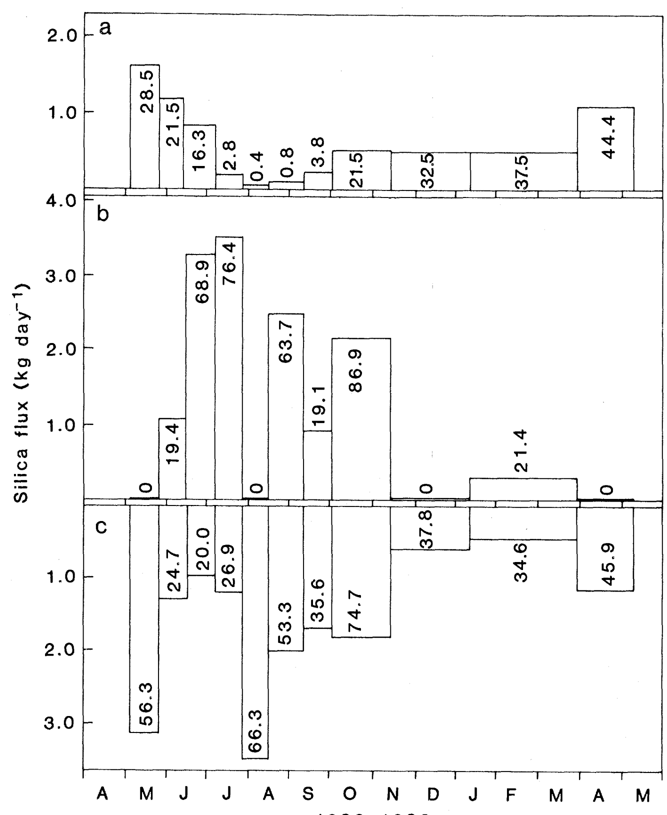
Flux	Silica: Total amount (kg $year^{-1}$)	Silica: DRS content (mg $liter^{-1}$)	Water (10^3 m^3 $year^{-1}$)
	Inputs		
Ground water	125 to 300*	4.9 to 7.4	21 to 39
Atmosphere (wet and dry)	0.7	0.002	346
Gross regeneration	200 to 510†		
	Outputs		
Ground water	1.3	0.010	127
Sedimentation‡			
Gross	380 to 570		
Net	200 to 375		

*See (*8, 13*). †Calculated from Eq. 1. ‡Gross sedimentation refers to the flux of settling PBS as measured with sediment traps (*9*). Net sedimentation refers to PBS permanently accumulated in the bottom sediments (*10*).

cycled in the lake approximately 2.5 times during the year, once through direct incorporation into diatom biomass and about 1.5 times through use of silica produced by regeneration. Analyses of bottom sediments indicate that the silica in the lake is approximately at steady state on an annual basis (input equals output). The net (permanent) accumulation of PBS in the "deep hole" sediments is about 4.6 g m^{-2} $year^{-1}$ and has not changed significantly over the last 175 years (*10*). The corresponding lakewide sediment accumulation rate (275 kg $year^{-1}$) is not significantly different from the ground-water input (210 kg $year^{-1}$).

Clearly, silica supplied from ground water is the ultimate control on silica cycling in Crystal Lake. Regeneration results in the reuse of silica originating in ground water and a corresponding increase in diatom production. Substantial production of diatoms also occurs during late summer and fall (Fig. 1, a and b). The main silica source during this period is regeneration. On an annual basis, ground water and regeneration sources of silica are approximately equal in their contribution to diatom production. Because ground water is the primary external silica source and silica is buried in bottom sediments, silica concentrations and diatom production in Crystal Lake

Fig. 2. Inputs and outputs of silica for Crystal Lake for the period May 1982 to May 1983: (a) ground-water inflow of dissolved reactive silica (total flux per year, 210 kg); (b) gross regeneration of total silica (355 kg); (c) gross sedimentation of particulate biogenic silica (475 kg). The height of each bar represents the flux in kilograms per day, and the value within the bar represents the total flux for the sampling interval. Although regeneration occurs throughout the year, sometimes the amounts are small as compared to the uncertainty in the mass balance equation. This leads to apparent zero regeneration values during periods of low regeneration.



would be reduced considerably in the absence of ground-water inflow. In addition, if a large fraction of the sedimented diatom silica were not regenerated, the diatom crop in Crystal Lake would be similarly reduced.

Ground water clearly is a major factor controlling the chemical composition and biological dynamics of certain lakes. The role of ground water will be dominant for some constituents and lakes (*14*) but may be minor in others (*15*). Thus, we concur with Winter (*3*) in recognizing the need for understanding ground water–lake relations when constructing lake nutrient and water budgets.

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6. Samples were collected at five to ten depths at the deep-hole station; see Fig. 1 for the collection frequency.
7. We determined DRS on 0.4-μm (Nuclepore) filtrates, following the method of J. D. H. Strickland and T. R. Parsons [*A Practical Handbook of Seawater Analysis* (Fisheries Research Board of Canada, Ottawa, 1972), pp. 65–70]. PBS was analyzed by the method of D. W. Eggiman, F. T. Manheim, and P. R. Betzer [*J. Sediment. Petrol.* **50**, 215 (1980)]. TS was calculated as DRS + PBS. Chlorophyll a was measured according to the method of C. J. Lorenzen [*Limnol. Oceanogr.* **12**, 343 (1967)].
8. Data from 57 piezometers around and beneath the lake were input into flow nets for Darcy's law calculations to determine the monthly ground-water flux to and from the lake.
9. Duplicate traps (3:1 ratio of depth to diameter) were deployed at 17 m; see W. D. Gardner [*J. Mar. Res.* **38**, 41 (1980)] for general design. The relative error between duplicate traps was about 20 percent. Lower accuracy is expected during the well-mixed periods (early May to mid-June and late October to mid-December).
10. The permanent accumulation rate was based on direct analysis of PBS in depth-sectioned sediment cores and a mass sedimentation rate measured by R. Talbot [thesis, University of Wisconsin–Madison (1981)] from excess ^{210}Pb profiles. The range reflects the uncertainty in the area of the depositional zone and the lateral changes in sediment PBS concentrations.
11. Rainfall was measured at a National Atmospheric Deposition Program site located 3 km from Crystal Lake. The mean DRS content was taken from unpublished data of S. J. Eisenreich, P. J. Emmling, and A. M. Beeton for bulk precipitation collected in the area.
12. A mixed-lake mass of 100 kg of silica corresponds to a concentration of about 25 μg liter^{-1}. For comparison, typical concentrations of DRS in northern temperate lakes are 0.46 to 1.18 mg liter^{-1} (*2*).
13. The accuracy of the calculated regeneration flux depends on errors in the other silica fluxes (Eq. 1), estimated to be about 30 percent for gross sedimentation, 50 percent for ground-water inflow, and 20 percent for ΔTS. Thus, errors in regeneration range from about 25 to 30 percent for high fluxes to >100 percent for low values. We constrained Eq. 1 to avoid negative regeneration values by adjusting gross sedimentation. We assume that PBS dissolution in the sediment traps is negligible.
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16. We gratefully acknowledge the critical discussions and manuscript reviews by T. Kratz, A. Beckel, T. Frost, and M. Anderson. Research support was provided through the NSF Long-Term Ecological Research Program, contract DEB 8012313.
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Geologic Youth of Galápagos Islands Confirmed by Marine Stratigraphy and Paleontology

Abstract. *Six distinctive types of fossiliferous marine deposits occur on the Galápagos Islands that provide evidence for the age of emergence of the islands above sea level and hence a maximum age for the islands' terrestrial biota. These subtidal to supratidal deposits include (i) volcanic tuffs with fossils, (ii) limestones and sandstones interbedded with basalt, (iii) terrace deposits, (iv) beach rock, (v) supratidal talus deposits, and (vi) recently uplifted tidal and subtidal rocks and sand. With the exception of (vi), the deposits were previously assigned ages varying from Miocene to Pleistocene, but all are less than about 2 million years old. This age, together with independently determined geologic ages, indicate that the islands emerged from the sea relatively recently and that all evolution of the islands' unique terrestrial biota occurred within the past 3 to 4 million years.*

The Galápagos Islands are famous for their unique terrestrial biota. Species there evolved in isolation and radiated into a variety of ecological niches. For example, 13 species of Darwin's finches radiated from an apparent single ancestral species (*1*). No fossil evidence has been uncovered that reveals the initial history or age of this biota, hence the earliest time of arrival of any ancestral species and the maximum time available for radiation on the islands can be established only from geologic and marine paleontologic evidence. To date, geologists have suggested that the islands are very young, perhaps no older than 3+ million years (*2, 3*), whereas paleontologists have suggested a Miocene age (10 to 14 million years ago) for some fossil occurrences and Pliocene to Pleistocene ages for others. Thus the age of the initial appearance of the islands above sea level and the time at which they first were available for colonization by a terrestrial biota have not been resolved. The reports of pre-Pleistocene ages based on marine fossils and sedimentary rocks are cited in biological arguments concerning the time of colonization and rates of evolutionary divergence in the fauna (*4*). We describe here six distinctive types of fossiliferous marine deposits that confirm the younger ages proposed by geologists (Figs. 1 and 2).

Marine fossils have long been known from the Galápagos Islands. Darwin (*5*) and Wolf (*6*) reported marine fossils in volcanic rocks high above sea level, but these reports were not investigated subsequently. Fossils reported to be Pleistocene and Pliocene were later described from various sedimentary deposits on several islands (*7–9*). The oldest age inferred for the Galápagos is Miocene and is based on fossils and stratigraphy of limestone deposits on northeastern Isla Santa Cruz (*10*). Radiometric dates (*3, 11–16*) and the islands' plate tectonic history (*2*), however, indicate that the islands did not begin to emerge from the sea until the Pliocene, some 3 to 4 million years ago.

On eight islands we found six types of fossiliferous marine deposits: (i) submarine tuff cones, (ii) limestone and sandstone interbedded with pillow basalts and basalt flows, (iii) subtidal rock and sand deposits preserved on terraces, (iv) beach rock, (v) supratidal talus debris, and (vi) recently uplifted subtidal to supratidal rocks and sand. These deposits bear significantly on the geologic history of the islands, and types (ii) through (iv) have been used in previous interpretations of the islands' age (Fig. 2).

The fossiliferous tuffs occur as broad cones formed during shallow submarine eruptions. Six major tuff cones and cone complexes ring Isla Santa Cruz (*15*) and are thought to represent an early phase of Galápagos volcanism (*16, 17*). The cones are now eroded and are connected to the volcanoes of the main island by subaerial basalt flows. We studied the tuff cones at Cerro Gallina and Cerro Colorado (Fig. 1) (*18*). In the poorly sorted and poorly bedded facies near the vents, boulder-sized fragments of shallow-water coquinas and fossiliferous limestone are incorporated in the tuff. In