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• To cite this version:

Anne Alexandre, Jean-Dominique Meunier, Fabrice Colin, Jean-Mathias Koud. Plant impact on the biogeochemical cycle of silicon and related weathering processes. Geochimica et Cosmochimica Acta, 1997, 61 (3), pp.677-682. 10.1016/S0016-7037(97)00001-X . hal-01909699

HAL Id: hal-01909699 https://hal.science/hal-01909699

Submitted on 17 Dec 2018

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PII S0016-7037(97)00001-X

LETTER

Plant impact on the biogeochemical cycle of silicon and related weathering processes

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(Received July 16, 1996; accepted in revised form November 1, 1996)

Abstract—The contribution of plants to the biogeochemical cycle of Si and related weathering processes was studied in an equatorial rainforest ecosystem (Congo) where the biologic turnover of Si is high (58 to 76 kg/ha/y). Litterfall leaves, a soil profile and groundwaters were analysed. Phytoliths and organic matter have a similar distribution with depth in the soil profile. The model of a bicompartmental distribution of organic matter is applied to phytolith distribution and shows that about 92% of the biogenic silica input is rapidly recycled while about 8% of the biogenic silica input supplies a stable pool of phytoliths, with a lower turnover. Reprecipitation of silica was observed at the base of the soil profile, indicating a local geochemical cycle of Si requires that the vegetation absorb dissolved silicon released from weathering of minerals, which otherwise would be available for mineral neoformation or export from the profile towards regional drainages. Plant uptake of Si increases the chemical weathering rate without increasing the denudation rate. This study shows that the uptake, storage, and release of Si by the vegetation have to be taken into account when using dissolved Si for tracing chemical weathering dynamics. *Copyright* © 1997 Elsevier Science Ltd

1. INTRODUCTION

Silicon (Si), the most common element of the Earth's surface after oxygen, is released in soil by chemical and biological processes (Iler, 1979), eventually reaching rivers where its amount is indicative of weathering rates (Meybeck, 1987; Bluth and Kump, 1994; White and Blum, 1995) and material mass balance (Wollast and Mackenzie, 1983). Earlier studies have recognized the potential for biomass storage and release of Si, but do not include a quantitative assessment of biological reservoirs in their results and models. Other studies have provided evidence of the effect of land plants on mineral weathering but without investigating the Si cycle (Knoll and James, 1987; Drever, 1994).

The biogeochemical cycle of Si, as a function of ecosystems, has been investigated by few authors (Bartoli, 1983; Lucas et al., 1993). Biogenic silica is not incorporated into soils in dissolved form, but as hydrated opal-A particles called phytoliths. Once Si is absorbed by the roots of many living higher plants, Si precipitates in plant tissues (a few ppm to 15% wt) as phytoliths, along cell walls or filling the cell lumen and the intercellular spaces. Phytoliths range from one to several tenths of micrometers in diameter. Because equatorial forests are among the most efficient vegetation types in recycling silicon (Lucas et al., 1993; Gautam-Basak and Proctor, 1983; Rose et al., 1993), we have choosen to study phytoliths in the litter and weathering system developed under an equatorial rainforest environment. The study area is located in the rainforest of the Mayombe Range (Dimonika, Congo, 4°S/12°30E). The climate is equatorial with an average annual rainfall of 1500 mm (Clairac et al., 1989). The weathering cover has formed from Proterozoic schists and quartzites, on the slope of a 400 m rounded hill.

The ferrallitic soil profile shows three main layers: (1) above the saprolite, from 215 to 130 cm depth, a red clayey layer, with relicts of parent rock structure, Fe-rich nodules and a few vertical root pores. Bleached clays occur between 140 and 130 cm depth; (2) from 130 to 60 cm depth, a brown-yellow clayey layer, with an aggregated structure. Relative to layer 1, parent rock fragments decrease in size and number, Fe-rich nodules disappear and the density of root pores increases; (3) from 60 to 0 cm depth, a brownish/ yellow sandy-clayey layer, with coarser aggregates. Schist and quartz fragments are scarce, except between 50 and 60 cm depth. Root pores become abundant. A 6 cm thick humic horizon occurs at the top of the profile, under a few cm thick litter.

Leaves and soil were sampled at the end of the dry season (November 1992). Litterfall leaves were collected on a trap, located 12m above the soil. Silicon in washed leaves was determined by Inductively Coupled Plasma (ICP) after digestion in LiBO₂ at 900°C and HCl, with a Random Standard Deviation (RSD) of about 10%. Carbon and nitrogen were analysed using a C-H-N analyser (RSD of about 1%), in order to estimate the maturity of the leaves (Bernhard-Reversat et al., 1978). The litter layer was also sampled in order to investigate root phytoliths.

The soil profile was sampled every 10 cm above 60 cm, and every 30 cm below. Separation of the 2–50 μ m fraction was done as part of the phytolith extraction procedure. The mineralogical and chemical compositions of the soil were determined by X-Ray Diffraction (XRD), and I.C.P (RSD: 5%). Bulk density measurement were done by volume displacement and used to estimate amounts of silicate minerals and phytoliths in the whole soil column. Organic carbon was analysed with a C-H-N analyser (RSD: 5%).

Phytoliths from leaves and roots were extracted after washing in HCl and organic matter oxidation using HNO₃ and HClO₄. 20 g of dry soil were traited for phytolith extraction: the $>50 \ \mu m$ fraction

^{2.} MATERIAL AND METHODS

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was removed by wet sieving, while the $<2 \,\mu$ m fraction was defloculated in a NaP₀₃ solution buffered at pH 6 and removed by decantation. Organic matter was oxidized using H₂O₂ at 90°C. Phytoliths were extracted from the 2–50 μ m fraction by densimetric separation using a ZnBr₂ solution fixed at a specific gravity of 2.3, dried, and weighed (Kelly, 1990). The extracted material was over 95% pure. The granulometric analysis showed that phytoliths are not contained in the >50 μ m fraction. As phytoliths from the clay fraction were not analysed, the soil phytolith amounts presented here are minimum values. Phytoliths were observed under a Scanning Electron Microscope (SEM) equipped with an Energy Dispersive Spectrometer (EDS), and counted under an optical microscope.

Six m depth groundwaters were sampled downslope during the dry season. The samples were filtered at 0.22 μ m. Dissolved Si was analysed using I.C.P (RSD: 10%) and used to estimate Si outflow from the soil profile.

3. RESULTS

In litterfall leaves, Si, C, and N contents are, respectively, $1.5 \pm 0.15\%$ wt, $49.7 \pm 0.5\%$ wt, and $1.37 \pm 0.01\%$ wt. The C/N ratio is 36 ± 0.72 . This value is close to the C/N ratio of young litter leaves collected during four years a few kilometers distant from our area (Schwartz, 1993). EDS spectra of the phytoliths from leaves (Alexandre et al., 1994) show the presence of a small amount of Al in addition to much Si.

The soil mineralogical data (Table 1A) displays a trend from the topsoil to the bottom of the profile of decreasing quartz content and increasing goethite, illite, and kaolinite content. Two mineralogical discontinuities are observed: (1) at 50–60 cm, an increase of quartz content can correspond to weathered quartz vein and (2) at 130–140 cm, the goethite content decreases while the kaolinite content increases. The kaolinite/illite ratio, which generally increases with extent of weathering, stays constant with regards to upper levels. This layer is especially rich in clays and in bleached clays.

Organic carbon content decreases significantly down to 50-60 cm, and remains relatively constant at greater depths, except between 130 and 140 cm, where it reaches a second maximum (Table 1A, Fig. 2A). The phytolith distribution shows similar tendencies (Table 1A, Fig. 2A). The soil nitrogen levels were below the error range (0.2% wt).

From the top to the bottom of the profile, the circular rugous morphotype (Fig. 1A), a phytolith from dicotyledon stems (Welle, 1976; Scurfield et al., 1974), accounts for 72 to 90% of the phytoliths counted (Fig. 1C). The circular crenate morphotype (Fig. 1A), a *Palmae* phytolith (Piperno, 1987), fluctuates in abundance but is always below 10% while the combined amount of all other phytoliths decreases from 25 to 4% (Fig. 1C). The latter group mainly includes $2-10 \,\mu$ m diameter shapeless phytoliths and, in lower proportions, dicotyledon silicified vessel and dumbel, elongated, point and fan-shaped grass phytoliths (Piperno, 1987; Twiss, 1992). At the base of the profile, the elongated morphotype remains present while the shapeless phytoliths are less abundant than at the top.

The EDS spectra of soil phytoliths and of litter phytoliths are similar, consisting almost entirely of Si. No phytoliths were found in roots of the litter layer.

Below 180 cm, some phytoliths are attached by bridges a few micrometer thick (Fig. 1B). The resultant particle does not resemble any known plant tissue anatomy. EDS analysis of the bridge shows it to be identical in composition to plant and soil phytoliths. The bridges are likely a result of the

Table 1. Soil data: A: Soil mineralogical composition; $<2 \mu m$ fraction; organic carbon (O.C.) and phytoliths (phyto.) contents; bulk density. B: Data for calculation of the soil biogenic components stock: partial stocks of Si derived from phytoliths (phyto. Si), total stock of Si derived from phytoliths including stable and labile pools of Si derived from phytoliths. Assuming a phytolith mean water content of 10% (Bartoli, 1981) equivalent to 0.37 moles of H₂O for 2 moles of SiO₂, the related Si amount accounts for 42% of the phytolith amount measured. For a layer, the percent of Si derived from phytoliths unltiplied by the bulk density (t/m³) and the thickness of the layer (m) gives a partial stock of Si derived from phytoliths (t/m²). Data are interpolated for non sampled depths. The total stock of Si derived from phytoliths is the sum of the partial stocks.

mple #	oth (cm)	72	0)	olinite	artz	ethite	шт Шт	0	,to.	ې بر		/to. Si	/to. Si	al stock	ble pool	oile pool
Sai	Del	SiO	III	Ka	ð	в	2 2	Ö	Чd	Bul	Del	μÅ	μÂ	Tot	Sta	Lat
	(cm)				(%wt.)					(t/m3)	(cm)	(%wt.)	(t/ha)	of Si	of Si	of Si
	RSD=5%											RSD=	5%	from	from	from
1	(0-10)	75,45	10,8	14,2	64,6	6,4	37,9	1,120	0,594	1,70	(0-10)	0,25	4,24	phyto.	phyto.	phyto.
2	(10-20)	72,73	11,3	15,1	61,1	7,0	38,4	1,070	0,520	1,70	(10-20)	0,22	3,71	(t/ha)	(t/ha)	(t/ha)
3	(20-30)	72,81	11,3	15,9	60,8	7,5	38,3	0,725	0,461	1,70	(20-30)	0,19	3,29			
4	(30-40)	71,60	11,2	14,3	60,5	9,6	45,9	0,605	0,399	1,74	(30-50)	0,17	5,83			
5	(50-60)	71,46	7,8	10,2	63,7	16,6	34,9	0,465	0,196	1,87	(50-60)	0,08	1,56	26.63	6.9	19.7
6	(60-70)	62,83	11,2	13,5	52,0	20,2	42,1	0,475	0,093	1,66	(60-90)	0,04	1.95	±1.33	±0.3	±1
7	(90-100)	55,60	14,5	18,8	40,7	24,4	33,8	0,485	0,065	1,90	(90-130)	0,03	2,07			
8	(130-140)	55,13	19,7	25,4	35,4	13,9	58,0	0,865	0,090	1,55	(130-180)	0,04	2,93			
9	(180-190)	43,19	30,3	22,6	19,5	23,4	41,7	0,455	0,046	1,47	(180-200)	0,02	0,56			
10	(205-215)	38,66	24,7	24,3	20,0	26,7	60,5	0,545	0,046	1,64	(200-215)	0,02	0,48			

В



Fig. 1. (A) SEM microphotograph showing *a palmae* phytolith (circular spiny) and dicot phytoliths (circular rugose). (B) SEM microphotograph showing soil phytoliths linked together by silicous bridges a few micrometers thick. (C) Phytolith diagram from the soil.

precipitation of amorphous silica in the soil. Underlying groundwaters contain 4 ± 0.4 mg/L of dissolved Si, and thus are undersaturated with amorphous silica.

4. DISCUSSION

The distribution of phytoliths throughout the soil profile involves two differents mechanisms: translocation (Colin et al., 1992) and dissolution (Bartoli, 1981, 1983). Translocation is attested by the presence of phytoliths at the bottom of the profile. If the translocation was the only process, the amount of phytoliths in the whole solum (26.6t/ha, Table 1B and Fig. 3) divided by the forest production would give the age of the beginning of the accumulation. It would also equal the age of the soil developed under the forest. The litter leaf production measured in the Mayombe forest is 2.9 to 3.8 t/ha/y (Schwartz, 1993). Considering a Si content of $1.5 \pm 15\%$ wt, the Si production of this fraction ranges from 43.5 \pm 4. to 57 \pm 6 kg/ha/y. As it represents about 75% of the total forest production (Geis, 1973; Lucas et al., 1993), the Si production of the forest ranges from 58 \pm 6 to 76 \pm 7 kg/ha/y. According to this hypothesis, the maximum age of the soil profile would be 458 years. Formation rates of lateritic soils developed in conditions similar to the Dimonika ones have been calculated from rates of residual gold particles dispersion (Colin et al., 1993). They range from 8 to 11 m per million years. With a similar formation rate, the 2.15 m depth soil profile at Dimonika would be 195 to 270 kyr old. The stock of phytoliths in the soil is therefore not consistent with a mechanism of translocation alone and implies that dissolution has occured.

The phytolith content versus organic carbon content has been plotted (Fig. 2B) in order to discuss the two distributions, in relation to soil development. Three patterns are clearly distinguishable: (1) From the top to 50-60 cm (points 1 to 5, Fig. 2B), the intense biological activity leads



Fig. 2. (A) Distribution of organic carbon and phytoliths in the soil profile. (B) Relation between soil organic carbon and phytolith distributions.



Fig. 3. (A) Bi-compartmental distribution of phytoliths by analogy with the bi-compartmental distribution of organic matter. (B) The mixing line (% circular rugous morphotype) = f(1/phytolith content). (C) The biogeochemical cycle of silicon (after Bartoli, 1983) at Dimonika. The soil biogenic components (Si stock derived from phytoliths) calculation is presented Table 1B. The stock of soil nonbiogenic components is estimated following the same calculation. It includes neoformations.

to rapid mineralization and humification of organic matter and a rapid dissolution of the more soluble phytoliths. The remaining less soluble particles are partially translocated; (2) From 60-70 cm to the bottom of the soil column (points 6, 7, 9, and 10, Fig. 2B), except at 130-140 cm, the biological activity becomes less effective and organic matter stabilizes. Amorphous silica precipitation below 180 cm shows that the soil solution is oversaturated with respect to amorphous silica and implies that phytoliths could not dissolve below this depth. The translocation processes are less intense but still present; (3) Between 130 and 140 cm (point 8, Fig. 2B), the high amount of clay creates a less impermeable layer impeding downward translocation and/or increases organic matter/phytoliths/clays aggregate stability (Bartoli, 1981). Possible occurrence of a buried surface at 130-140 cm is not in agreement with the kaolinite/illite ratio distribution through the profile.

The circular rugous morphotype is the only dicot morphotype that is substantially preserved in the soil. Three causes can be responsible for the increase with depth of the amount of the circular rugose morphotype (Fig. 1C): (1) A higher rate of translocation due to its circular morphology; however, the presence of phytoliths with greater lengths and the small amount of $2-10 \ \mu m$ shapeless phytoliths at the base of the soil argue against the hypothesis of a morphological determining factor; (2) A forest opening could induce a decrease of the circular rugose abundance from the base to the top of the soil profile. This hypothesis is rejected because of the too low abundance of *Poaceae* phytoliths (Alexandre et al., 1995); (3) A higher resistance of the circular rugose morphotype to dissolution during its translocation through the soil profile.

The distribution of organic carbon is in agreement with previous studies of organic matter in many temperate and tropical soils (Balesdent and Guillet, 1982; Schwartz, 1991; Schwartz et al., 1992). The bicompartment model (Jenkinson and Rayner, 1977; Parton et al., 1987), assessed by ¹⁴C dating and δ^{13} C analysis (Balesdent and Guillet, 1982; Balesdent et al., 1987; Martin et al., 1990; Schwartz, 1991; Schwartz et al., 1992), assumes two pools of organic matter: one pool with a rapid turnover is maintained in dynamic equilibrium with litter inputs. Because of translocation and of a rapid turnover, this pool decreases from the top of the profile to trace levels at the bottom. A second organic pool is more stable and inactive over an ecological time scale. Because of translocation and of its stability, it remains constant through the solum. The mixing hypothesis is attested by the mixing line equation (α): (α) δ^{14} C or δ^{13} C = f(1/2)organic carbon content) (Balesdent and Guillet, 1982; Schwartz, 1991; Schwartz et al., 1992).

Biochemical data on soil organic matter decomposition, humification and stabilization support the bicompartmental model (Anderson, 1992). The stability of soil organic matter components depends on (1) the amount of recalcitrant humic polymers with high molecular weight and (2) the functionality of compounds and their potential complexation by clays and Al/Fe oxides (Jenkinson and Rayner, 1977; Parton et al., 1987; Anderson, 1992; Kögel-Knabner, 1992). In ferrallitic soils, the organic matter content is low, due to rapid decomposition, high mineralization, and low humification. But organic components are characterized by a high amount of humin and humic components highly aggregated with clays and iron oxides (de Boissezon, 1973; Boyer, 1982), which may supply a stable pool of organic matter.

By analogy with the bicompartmental model of the distribution of organic matter, the distribution of phytoliths may be modelled in a similar way (Fig. 3A). One pool of young phytoliths would be rapidly dissolved and recycled by vegetation. This pool decreases with depth to reach zero abundance at the base of the soil profil. The second pool of more stable phytoliths would remain constant with depth and represents the whole phytolith content of the base of the soil profile. This pool can be considered as particles output from the biological cycle of Si. Its increasing proportion with depth follows the circular rugose morphotype distribution. The mixing hypothesis between a young labile pool and a mature stable pool of phytoliths is attested by the mixing line equation (β): (β) (% circular rugous morphotype) = f(1/phytolith content) with linear $r^2 = 0.77$ (Fig. 3B). According to this hypothesis, the pool of stable phytoliths accounts for 7.5% of the phytolith input from the litter to the upper layer of the latosol, while 92.5% of phytolith input is rapidly dissolved (Table 1B, Fig. 3A).

A biogeochemical cycle of Si (Bartoli, 1983) may be developed and applied at Dimonika, based on a steady state system (Fig. 3C). Four reservoirs are defined: (1) the forest live biomass, (2) the soil biogenic components (Table 1B), (3) the soil nonbiogenic components, (4) the dissolved exchangeable biogenic and nonbiogenic components in soil waters. Input flows of Si are (1) forest production, (2) phytolith dissolution, and (3) the silicate mineral weathering release. Output flows of Si are (1) the phytolith preservation in the solum, (2) the uptake by the forest, and (3) the underground water flow and the Si uptake for neoformations of soil minerals.

Silicon accretion and Si input by rainfall are presumed lower or equal to 1 kg/ha/y according to data on other rainforest ecosystems (Bernhard-Reversat et al., 1978; Lucas et al., 1993). They are neglected in our calculations.

The Si forest uptake is estimated to be similar to the Si forest production (58 \pm 6 to 76 \pm 7 kg/ha/y). The Si flow from phytolith dissolution and the Si output derived from phytolith preservation account respectively for 7.5 and 92.5% of the litter input, or for 4 ± 0.4 to 6 ± 0.6 kg/ ha/y and 54 \pm 5 to 70 \pm 7 kg/ha/y. The Si soil water output is estimated from the groundwater Si content (4 \pm 0.4 mg/L) and the annual drainage (393 mm/y) calculated from annual rainfall (1,500 mm/y, Clairac et al., 1989), annual interception (300 mm/y) accounted for 20% of annual rainfall (Bernhard-Reversat et al., 1978), and annual evapotranspiration (807 mm/y) calculated according to Turc formula equation (Bernhard-Reversat et al., 1978). It reaches 16 \pm 1.6 kg/ha/y. The Si input resulting from silicate mineral weathering is equal to the Si input from phytolith dissolution $(54 \pm 5 \text{ to } 70 \pm 7 \text{ kg/ha/y})$ minus the sum of Si output in soil water ($16 \pm 1.6 \text{ kg/ha/y}$) and of Si uptake by the forest $(58 \pm 6 \text{ to } 76 \pm 7 \text{ kg/ha/y})$. It represents 20 to 22 kg/ ha/y and is the input from the dissolution of silicates minus any output due to neoformation of secondary silicates which cannot be estimated.

The resultant model of the Si cycle (Fig. 3C) shows that the Si release from phytolith dissolution is twice that of Si release due to silicate weathering. This result reflects the steady state between a low stock of biogenic silica (phytoliths) with high rates of dissolution and a much higher stock of nonbiogenic silicates with lower rates of dissolution. Because of the preservation in the soil of 7.5% of the phytolith production, the Si release from the dissolution of phytoliths is not sufficient for the forest uptake, and 4 ± 0.4 to 6 ± 0.6 kg/ha/y of Si absorbed need to be derived through weathering of soil minerals. This value represents 20 to 27% of the total weathering release.

Schematically, without vegetation, silicate dissolution (b) equals the sum of the Si output in waters (d) and of the Si output for neoformation (d'). The presence of vegetation may have different consequences for the cycle at steady state: (1) Forest uptake (c) equals phytolith dissolution (a)and does not change the Si output in waters (d), the Si output for neoformations (d'), and silicate dissolution (b). In other words, the system is not perturbed by the vegetation. This case occurs in ecosystems with vegetation deficient in Si or with soil environments favouring silicate dissolution (Bartoli, 1983); (2) Forest uptake (c) is more than phytolith dissolution (a), which involves either a decrease of the Si output in waters (d) and of the Si output for neoformation (d') or/and an increase in silicate dissolution (b). This case occurs in the rainforest ecosystem of Dimonika. The vegetation will increase the chemical weathering rate without increasing the denudation rate equivalent to the soluble Si percolating in the solum and removed out of the profile towards regional drainages. The resultant transport-limited landscapes are characteristic of humid tropical environments.

Acknowledgments—This work was supported by ORSTOM and the French programme P.E.G.I. The authors thank R. J. Gilkes, B. Hamelin, D. Nahon, C. Parron, D. Schwartz, and V. Targulian for their helpful corrections and suggestions, G. Kelly for his teaching on phytolith extraction procedure, F. Marseille for helpfull discussions about organic matter, and J. Fages for logistic support. The manuscript was improved by R. A. Berner and an anonymous reviewer.

Editorial handling: J. D. Macdougall

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