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The weathering stage of tropical soils affects the soil-plant cycle of silicon, but depending on land use

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ABSTRACT

Plants take up silicon (Si) from soil solution, and form biogenic silica bodies (phytoliths) that return to soil with plant debris. Since phytolith dissolution releases plant available Si, the soil-plant Si cycle tremendously influences the global Si cycle. Si plant uptake ranges from 0.7 to 1470 kg ha^{-1} year^{-1} among different terrestrial ecosystems depending on soil properties and processes, climate, plant species, and management practices. The humid tropics shelter a huge variety of soils. Many of them are strongly weathered and desilicated, and exhausted in plant nutrients. Nevertheless, these soils support evergreen forests with the greatest biodiversity and biomass because of an intense pumping of nutrients. This pumping involves non-essential Si, and further governs the soil-plant Si cycle, which is perturbed after converting forest area into cropland. Here, we used literature data quantifying the Si soil-plant cycle in natural forest areas and croplands established on soils that differ in weathering stage. We particularly focused on comparing forest to Si-accumulating rice crop. We show that the impact of soil weathering stage on the soil-plant Si cycle markedly differs depending on land use in the tropics. In slightly or moderately weathered soils, cultivated plants take up Si in larger amounts than forest trees do, likely because the former are stimulated to pump nutrients and dissolve Si from less soluble lithogenic and pedogenic silicates. With increasing soil weathering and desilication, Si plant uptake increases in natural forest ecosystems while it decreases in cultivated ecosystems. Four factors may explain this discrepancy: (i) since they are more soluble than lithogenic and pedogenic silicates, phytoliths make the pool of plant available Si; (ii) forest litter, which is densely exploited by roots, is a place of intense mineral pumping; (iii) deep rooting of forest trees enhances pumping too; (iv) crop harvesting exports Si out of cultivated ecosystems.

1. Introduction

Silicon (Si) is the second mass abundant element in the Earth's crust (28.8% wt) after oxygen (Wedepohl, 1995). In soils, total Si content ranges from 5 to 470 g kg^{-1} depending on soil mineralogy (McKeague and Cline, 1963) whereas the content of plant available Si varies from 3×10^{-3} to 4.5×10^{-1} g Si kg^{-1} (Liang et al., 2015). In shoot plant tissues, the mean Si concentration ranges between 1 and 100 g Si kg^{-1} and may exceed that of major nutrients (Hodson et al., 2005).

Despite the huge silicate mineral reserve in the Earth's crust, only a small portion of Si is mobile within the biogeochemical cycle of Si (Conley, 2002; Sommer et al., 2006). This cycle plays numerous ecological roles related to eminent global problematics and provision of ecosystem services, as illustrated through three examples. The global Si cycle is linked to the carbon (C) cycle (a.o. Goudie and Viles, 2012; Street-Perrott and Barker, 2008; Tréguer and Pondaven, 2000; Tréguer et al., 2018). In terrestrial ecosystems, mineral weathering consumes carbonic acid from dissolved carbon dioxide (CO_2) and releases monosilicic acid ($H_4SiO_4^0$ or dissolved silicon - DSi) and other solutes. Once DSi is transferred to watersheds and reaches marine ecosystems, it acts as a major nutrient for diatoms, and thus impacts the capacity of oceans to fix C (a.o. Ragueneau et al., 2006; Tréguer and Pondaven, 2000; Tréguer et al., 2018). In coastal areas, the ratio of Si to nitrogen (N) and phosphorus (P) in continental waters is a crucial factor in eutrophication (Cloern, 2001; Schelske and Stoermer, 1971). Eventually, Si is beneficial in protecting plants against biotic and abiotic stresses (see Coskun et al., 2019 for a review).

In a pioneer work, Bartoli (1983) reported the crucial role of plants in the biogeochemical cycle of Si and related soil weathering processes in temperate deciduous forests. He demonstrated that the biological cycling of Si controlled Si release from mineral weathering. Further studies confirmed the importance of the biological pumping in controlling the biogeochemical Si cycle (Alexandre et al., 1997; Derry et al., 2005; Lucas et al., 1993; Meunier et al., 1999). Compiling

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literature data, Cornelis and Delvaux (2016) proposed that plant impact depended on soil weathering stage in natural ecosystems, highlighting an increased biological Si feedback loop with increasing weathering stage.

The conversion of forest areas into croplands alters the biogeochemical cycle of Si (a.o. Clymans et al., 2011; Guntzer et al., 2012; Keller et al., 2012; Struyf et al., 2010; Vandevenne et al., 2011). Actually, this transition results in the exhaustion of the soil phytolith pool (Barão et al., 2014; Guntzer et al., 2012; Struyf et al., 2010; Vandevenne et al., 2015). It also decreases the plant available Si pool (Klotzbücher et al., 2015a; Savant et al., 1996; Struyf et al., 2010), and the Si fluxes to watersheds (Struyf et al., 2010), thus affecting the ecological functions of Si. Thus, in croplands, the biological Si feedback loop would decrease with increasing soil weathering stage. Indeed, in tropical banana and rice croplands, plant accumulation of Si decreases with increasing soil weathering stage (Henriet et al., 2008a,b; Klotzbücher et al., 2015a; Tavakkoli et al., 2011). In natural ecosystems, on the contrary, the biological feedback loop of Si increases with increasing degree of alteration (Cornelis and Delvaux, 2016).

Here we test the idea that land use may affect the relationship between plant Si accumulation and soil weathering stage in the tropics. We use published data collected in humid tropical regions worldwide. We particularly focus on comparing forest to Si-accumulating rice crop. We first recall that the soil-plant cycle of Si is constrained by the dissolution of weatherable minerals in slightly to moderately weathered soils (Section 2) and by that of phytoliths in highly weathered soils (Section 3). Next, we focus more specifically on the control of the Si soil-plant cycle in natural ecosystems (Section 4) and then in croplands (Section 5). Finally, we discuss the impact of soil weathering stage on this control in both types of ecosystems (Sections 6, 7, 8), in order to highlight the respective impacts of soil weathering stage and land use on the soil-plant cycle of Si.

Our methodological approach is based on the use of published data and their statistical processing. In particular, we have identified Si uptake data, as well as climate and soil types in tropical regions. The soils have been categorized according to their weathering stage, identifiable via the mineral reserve or taxon. We performed descriptive statistics, mainly using the ggplot function of the R programming language. We then discuss the data based heavily on well-known mechanisms and soil processes.

2. Mineral dissolution controls the Si soil-plant cycle in slightly to moderately weathered soils

As illustrated in Fig. 1, the continental cycle of Si is mainly based on the Si soil-plant cycle where the original source of Si is the reserve of primary weatherable lithogenic silicates (LSi) (Alexandre et al., 1997; Henriet et al., 2008b; McKeague and Cline, 1963). In soils undergoing net acidification (van Breemen et al., 1983), LSi dissolution releases aqueous $H_4SiO_4^0$ (dissolved Si: DSi), aluminum (Al), iron (Fe) and other solutes. The fate of DSi may take four main routes: (i) leaching and export to watersheds; (ii) synthesis of pedogenic silicates (PSi) through the formation of clay minerals (Garrels and Christ, 1965) and/or amorphous silica (Drees et al., 1989); (iii) adsorption on Fe and Al oxides (Beckwith and Reeve, 1963; Jones and Handreck, 1963; McKeague and Cline, 1963); (iv) uptake by plant roots (Jones and Handreck, 1965).

According to Cornelis and Delvaux (2016), both the LSi dissolution and PSi neoformation [routes (i) and (ii)] govern the mobility of Si in slightly to moderately weathered soils. At advanced weathering stage, Al and Fe oxides accumulate whereas silica exhaustion vanishes the contribution of LSi and PSi silicates to the pool of plant available Si [route (iv)]. The latter pool is fed through phytolith dissolution (Lucas et al., 1993), hence creating a biological Si feedback loop, thus inducing a steady state (Alexandre et al., 1997).

3. The biological Si feedback controls the Si soil-plant cycle in highly weathered soils

The **biological Si feedback loop** encompasses the processes of plant uptake of Si, phytolith formation in plant tissues, return to soil, and dissolution to feed the plant available Si reservoir (Alexandre et al., 1997).

Briefly, once taken up by plant roots, $H_4SiO_4^0$ is translocated to shoots through the transpiration stream (Mitani and Ma, 2005). At transpiration sites, water evaporation provokes $H_4SiO_4^0$ oversaturation with respect to amorphous Opal A silica ($SiO_2.nH_2O$) named phytolith (PhSi) (Piperno, 1988; Raven, 1983, 2001; Sangster and Hodson, 1986).

Plant species take up Si through: active, passive or rejective mechanisms (Ma and Takahashi, 2002; Ma et al., 2001, 2006), and are classified as Si high-, intermediate-, or non-accumulating plant species, respectively. Thus, plant Si uptake considerably varies from 0.7 to 1470 kg ha^{-1} yr^{-1} (Table 1). In temperate forest ecosystems, it ranges from 2 to 44 kg Si yr^{-1} depending on tree species and soil type (Bartoli, 1983; Cornelis et al., 2010; Farmer et al., 2005; Fulweiler and Nixon, 2005; Gérard et al., 2008; Markewitz and Richter, 1998; Sommer et al., 2013). In humid tropical forests, Si uptake by trees varies from 7 to 76 kg ha^{-1} yr^{-1} (Alexandre et al., 1997; Lucas, 2001; Lucas et al., 1993; Meunier et al., 2010), and even from 450 to 957 kg ha^{-1} yr^{-1} in the particular case of bamboo forest (Li et al., 2006; Meunier et al.,

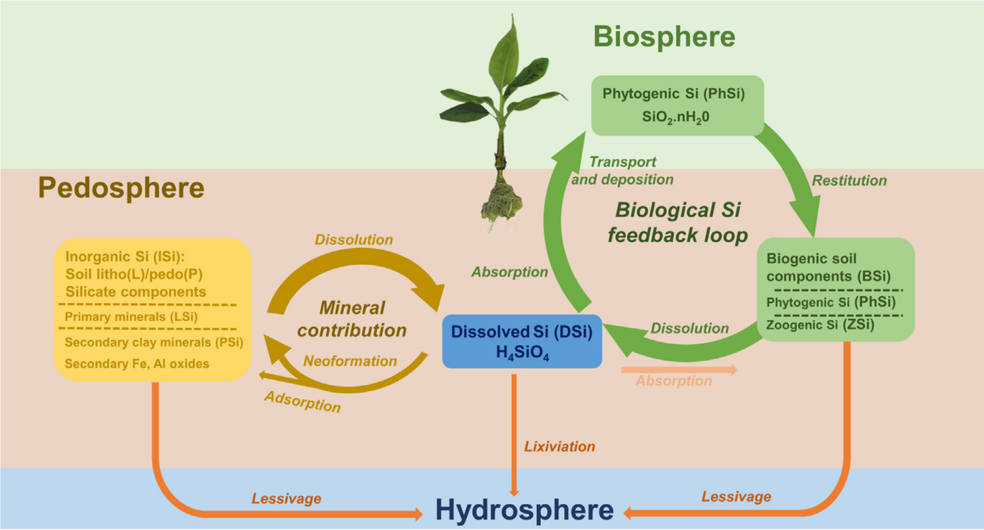

Fig. 1. Dissolved Si (DSi) originates from the inorganic Si and biogenic Si pools. DSi can follow four routes: (i) leaching and export to watersheds; (ii) PSi synthesis through the formation of clay minerals and/or amorphous silica; (iii) adsorption on Fe and Al oxides; (iv) uptake by plant roots. Adapted from Cornelis and Delvaux (2016).

Table 1
Experimental values of Si uptake by plants in forest, grass and cultivated ecosystems.

Ecosystem	Si uptake ($kg\,ha^{-1}\,yr^{-1}$)	References	Ecosystem	Si uptake ($kg\,ha^{-1}\,yr^{-1}$)	References
Forest ecosystems			Cultivated ecosystems		
Tropical forest	7	Meunier et al. (2010)	Triticale	36–44	Vandevenne et al. (2011)
Tropical forest	21	Lucas (2001)	Flax	0.7–0.9	Vandevenne et al. (2011)
Tropical forest	40–50	Lucas (2001)	Barley	15–24	Vandevenne et al. (2011)
Tropical forest	58	Alexandre et al. (1997)	Barley	99	Tubana et al. (2016)
Tropical forest	76	Alexandre et al. (1997)	Maize	112–127	Vandevenne et al. (2011)
Bamboo forest	450–670	Meunier et al. (1999)	Maize	129	Tubana et al. (2016)
Bamboo forest	957	Li et al. (2006)	Oat	19–27	Vandevenne et al. (2011)
Bamboo forest	77–330	Umemura and Takenaka (2014)	Oat	48	Tubana et al. (2016)
Coniferous forest (Black pine)	2.3	Cornelis et al. (2010)	Sorghum	62	Tubana et al. (2016)
Coniferous forest (Douglas fir)	30.6	Cornelis et al. (2010)	Soybean	59	Tubana et al. (2016)
Coniferous forest (Spruce)	43.5	Cornelis et al. (2010)	Sugar beet	3–8	Vandevenne et al. (2011)
Coniferous forest (Fir)	35.7	Farmer et al. (2005)	Sugar beet	1408	Tubana et al. (2016)
Coniferous forest (Pine)	7.9	Farmer et al. (2005)	Wheat	37–113	Vandevenne et al. (2011)
Coniferous forest	8	Bartoli (1983)	Wheat	108	Tubana et al. (2016)
Coniferous forest (Douglas fir)	44.4	Gérard et al. (2008)	Wheat	94	Guntzer et al. (2012)
Mixed forest beech and pine	35	Sommer et al. (2013)	Wheat	20	Guntzer et al. (2012)
Mixed forest beech and fir	25.8	Farmer et al. (2005)	Rice	329	Tubana et al. (2016)
Deciduous forest (Beech)	23.3	Cornelis et al. (2010)	Rice	270	Desplanques et al. (2006)
Deciduous forest (Oak)	18.5	Cornelis et al. (2010)	Rice	500	Makabe et al. (2009)
Deciduous forest (Beech)	36.5–46.3	Farmer et al. (2005)	Rice	218	Yang and Zhang (2018)
Deciduous forest	26	Bartoli (1983)	Rice	1470	Klotzbücher et al. (2016)
Grass ecosystems			Rice	1140	Klotzbücher et al. (2016)
Temperate grassland	87–215	Melzer et al. (2010)	Rice	600	Klotzbücher et al. (2016)
Temperate grassland	22	Blecker et al. (2006)	Rice	600	Klotzbücher et al. (2016)
Temperate grassland	26	Blecker et al. (2006)	Rice	360	Klotzbücher et al. (2016)
Temperate grassland	55	Blecker et al. (2006)	Rice	28–390	Klotzbücher et al. (2016)
Temperate grassland	56	Blecker et al. (2006)	Rice	370–470	Klotzbücher et al. (2016)
Temperate grassland	58	Blecker et al. (2006)	Rice	234	Prakash et al. (2011)
Temperate grassland	59	Blecker et al. (2006)	Rice	130	Prakash et al. (2011)
Temperate grassland	67	Blecker et al. (2006)	Sugarcane	160	Tubana et al. (2016)
Temperate grassland	12	White et al. (2012)	Sugarcane	248	Ross et al. (1974)
Temperate grassland	18	White et al. (2012)	Sugarcane	408	Ross et al. (1974)
Temperate grassland	23	White et al. (2012)	Sugarcane	379	Samuels (1969)
Temperate grassland	46	White et al. (2012)			
Temperate grassland	48	White et al. (2012)			
Tropical savanna	98–552	Melzer et al. (2010)			
Tropical savanna	127	Alexandre et al. (2011)			

1999). The Si uptake by grasses ranges from 12 to 67 $kg\,ha^{-1}\,yr^{-1}$ in dry and humid temperate grasslands (Blecker et al., 2006; White et al., 2012), and from 98 to 552 $kg\,ha^{-1}\,yr^{-1}$ in intertropical savannas (Alexandre et al., 2011; Melzer et al., 2010). In croplands, Si uptake by cultivated plants varies widely from 0.7 to 1470 $kg\,ha^{-1}\,yr^{-1}$ depending on plant species and environmental conditions (Desplanques et al., 2006; Guntzer et al., 2012; Klotzbücher et al., 2016; Makabe et al., 2009; Prakash et al., 2011; Ross et al., 1974; Tubana et al., 2016; Vandevenne et al., 2011; Yang and Zhang, 2018).

The global annual production of phytogenic Si (PhSi) by higher plants ranges from 1.7 to 5.6 × 10^{12} kg Si yr^{-1} (Conley, 2002; Laruelle et al., 2009), and rivals with that of biogenic Si (BSi) production by diatoms in oceans (6.7 × 10^{12} kg Si yr^{-1}) (Treguer et al., 1995).

The quantity of soil PhSi commonly ranges from < 1 to 30 $g\,kg^{-1}$ on a total soil basis (Drees et al., 1989), but is above 50 $g\,kg^{-1}$ in a number of soils (Clarke, 2003). Actually, it depends on soil type, but also on the type of terrestrial ecosystem, which influences the Si cycling. The largest PhSi amounts are measured in soils of coastal and inland swamps, flood plains, grasslands and forests (Clarke, 2003). In natural climax ecosystems, the annual Si returns from plant to soil matches the annual Si plant uptake, hence reaching steady state (e.g. Alexandre et al., 1997; Sommer et al., 2013). Once climax is not reached, and if net above-ground biomass productivity is above biomass return to soil, PhSi return is generally below plant Si uptake (Meunier et al., 2010). In agricultural ecosystems, crop harvesting reduces the restitution of PhSi to soil (Vandevenne et al., 2011).

PhSi particles readily dissolve at common soil solution pH values (Fraysse et al., 2009, 2010). Their dissolution rate is 1 to 100 order of magnitude higher than that of LSi and PSi minerals, and decreases with increasing acidity (Fraysse et al., 2006, 2009, 2010), as well as increasing salinity (Loucaides et al., 2008). Thus, only a small part of annual PhSi deposition remains undissolved (~8% in tropical forests (Alexandre et al., 1997)). Since phytolith dissolution depends also on plant species (Alexandre et al., 1997; Blecker et al., 2006; Li et al., 2014; Wilding and Drees, 1974), the origin of phytoliths influences the contribution of PhSi to the DSi pool at given pH. For example, the proportion of DSi released from phytolith dissolution ranges from ~10–30% in pine forests and forest tundra (Bartoli, 1983; Pokrovsky et al., 2005), but to ~90% in forested Hawaiian watersheds (Derry et al., 2005; Street-Perrott and Barker, 2008).

Fig. 2 illustrates that the biological Si feedback loop progressively takes over the mineral contribution to Si plant uptake (Table 1 in Cornelis and Delvaux, 2016). Based on this model, we redraw the Q-I relationship for natural ecosystems in Fig. 3b. In slightly weathered soils, LSi/PSi mineral dissolution/neoformation processes control the activity of $H_4SiO_4{}^0$, and thus govern the Si soil-plant cycle (Fig. 3b-(1)). LSi depletion leads to the progressive increase in the PhSi pool, which is largest in highly desilicated soils (Fig. 3b – from (1) to (4)).

Humid tropical regions conditions of temperature and rainfall promote mineral weathering and loss of silica. A number of soils in the humid tropics are highly weathered, since they cover $> 50\%$ of the humid tropical areas (Sanchez, 2019), notably in central Africa. Their mineral assemblage consists of residual unalterable primary minerals, and neoformed secondary minerals typical for desilicated soils such as kaolinite, gibbsite, hematite, and goethite. In the humid tropics, slightly weathered soils mostly occur in areas affected by recent tectonic faulting and subsequent rock outcropping, and/or volcanic activity (e.g. the African Great Lakes Region, Caribbean, Central and South America,

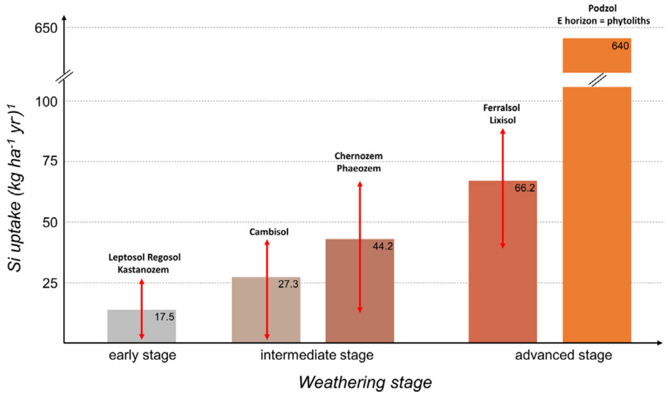

Fig. 2. Impact of soil weathering stage on plant Si uptake as measured in various natural ecosystems: forest and prairie in Leptosol, Regosol, Kastanozem; forest in Cambisol, prairie in Chernozem and Phaeozem; rainforest and tall savanna in Ferralsol and Lixisol, bamboo forest in Podzol. In each box, the arrow represents the range of values; the figure is the average value of Si uptake as computed from Table 1 in Cornelis and Delvaux (2016).

Indonesia, Philippines…).

Highly weathered soils in the humid tropics are well-known to support the growth and development of the densest forests with the greatest biomass and biodiversity in the world (Beer et al., 2010; Laliberté et al., 2013; Myers, 1988) because mineral fertility is concentrated in forest biomass and litter. Once deforested and used for cropping, these ferrallitic soils are widely recognized as unfertile soils (Sanchez, 2019). In contrast, little weathered soils in the humid tropics are highly fertile and productive, and they can support high yielding crops (Sanchez, 2019). Thus, in the tropics, soils may react differently to the conversion of forest to cropland according to their weathering stage. In particular, the soil-plant Si cycle may differ depending on weathering stage but also on land use.

4. The Si soil-plant cycle in humid tropical forests

4.1. In forests on slightly weathered soils, mineral dissolution controls the Si soil-plant cycle

In the young volcanic soil of the Marelongue reserve (Réunion Island), the soil-plant Si cycle was not dominated by the biological Si feedback loop because basalt weathering and wood storage of nutrients were still active processes (Meunier et al., 2010) (Table 2). The input from dying trunks was not significant in such a young forest unlike older tropical forest (Lucas et al., 1996). The elemental biocycling in the Marelongue reserve depended on plant species for both the litterfall and wood storage (Meunier et al., 2010). The four tree species that contributed mostly to litterfall (70%) represented only 45% of the annual Si biocycling, while one species contributing to 2% of the litterfall represented 13.2% of the annual Si biocycling. In this ecosystem, the leaching output of Si was 15 kg ha^{-1} yr^{-1}, i.e. about twice the restitutions of Si by litterfall. Meunier et al. (2010) explained it by a combination of two factors enhancing weathering: the basaltic nature of the parent-rock rich in weatherable silicates, and the hot and wet conditions. In agreement with Meunier et al. (2010), Yang and Zhang (2018) demonstrated that the Si cycle in forests on slightly altered Leptosols and Cambisols was more dependent on the dissolution of LSi minerals than on the recycling of Si by plants (Table 2). In these little weathered humid tropical soils, the Si cycle was thus characterized by high LSi dissolution rates that led to large Si outputs by leaching, and a virtually absent biological Si feedback loop.

4.2. In forests on highly weathered soils, the biological Si feedback loop controls the soil-plant Si cycle

At advanced stage of weathering in humid tropical conditions, the soil mineralogical assemblage includes residual LSi minerals that resist to weathering (e.g. quartz, muscovite), kaolinite and secondary Al and Fe oxides (e.g. gibbsite, goethite, hematite). Ferralsols, Lixisols, Acrisols, and Podzols are typical highly weathered soils of the humid tropics. Alexandre et al. (1997) and Lucas et al. (1993) showed that the biological Si feedback loop was crucial to maintain the Si “fertility” in

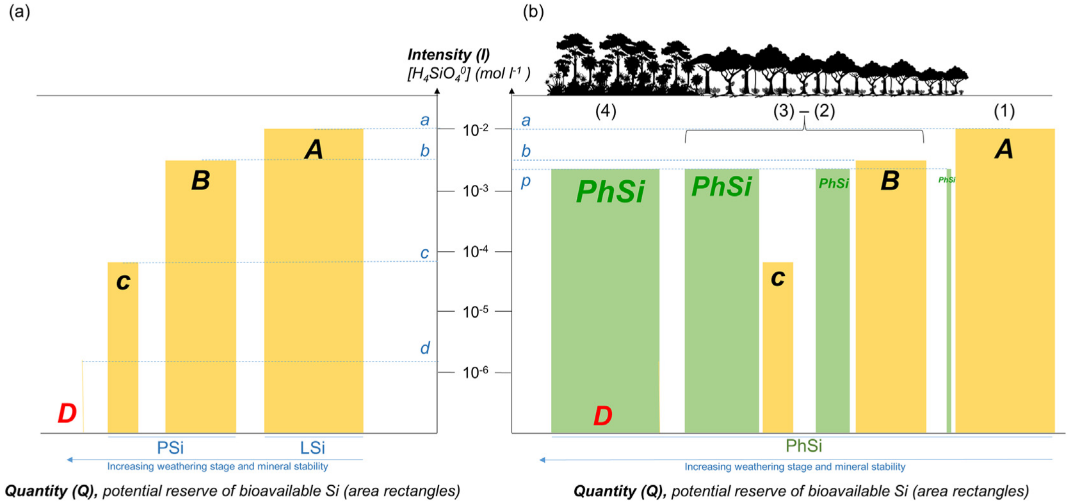

Fig. 3. (a) The Si quantity-intensity (Q-I) relationship exclusively considers the mineral contribution. With increasing weathering, successive LSi (A) and PSi (B, C) dissolution controls the activity of aqueous $H_4SiO_4^0$ at different levels ($> 10^{-4}$ M). Upon PSi exhaustion, secondary oxides are devoid of Si (D), hence the activity of aqueous $H_4SiO_4^0$ is very low ($< 10^{-4}$ M). (b) The Si Q-I relationship considers both the mineral contribution and biological Si feedback loop, the concomitant evolution (1–4) of the ecosystem being schematized. (1) At early stage of weathering, LSi/PSi mineral dissolution/neoformation governs plant Si uptake. Upon gradual development of forest ecosystem (2–3) and intermediate weathering stage, biological pumping and soil PhSi pool increase. At advanced weathering (4), the PhSi pool is largest, while the forest climax stage is reached. The biological Si feedback loop takes over the mineral contribution, and the PhSi pool alleviates natural soil desilication (Lucas et al., 1993). The size of each rectangle represents the related Si stock.
Adapted from Cornelis and Delvaux (2016).

Table 2
Experimental values of Si uptake, Si restitution and Si export rates, and Si in standing biomass in various forest and agricultural ecosystems as measured in the above-ground plant parts. Values for croplands are given for soils that did not receive any Si amendments. Si uptakes are lower for the tropical forests on slightly weathered soils than for the tropical forests established on highly weathered soils. Inversely, values of Si uptake are globally larger for the croplands on slightly weathered soils than for the croplands on highly weathered soils. The data present here below are published experimental data from field studies.

Ecosystem	Climate (MAP in mm)	Soil weathering degree		Location	Si uptake ($kg\,ha^{-1}\,yr^{-1}$)	Si restitution ($kg\,ha^{-1}\,yr^{-1}$)	Si export ($kg\,ha^{-1}\,yr^{-1}$)	Si in standing biomass ($kg\,ha^{-1}$)	Reference
		WRB class	TRB[a]						
Weakly weathered soils									
Rain forest	Tropical humid (4200)	Leptosol		Reunion Island	7	7	0	17.76	Meunier et al. (2010)
Coniferous forest	Subtropical monsoon (1585)	Leptosol Cambisol		Anhui Province (China)	28	17.5	0		Yang and Zhang (2018)
Rice	Subtropical monsoon (1585)	Cambisol		Anhui Province (China)	218	177.4	41		Yang and Zhang (2018)
Rice	Tropical monsoon (2050)		168	Luzon Island (Philippines)	1470	230	1240	560–760	Klotzbücher et al. (2016)
Rice	Tropical monsoon (2050)		176	Luzon Island (Philippines)	1140	240	900	510–630	Klotzbücher et al. (2016)
Rice	Tropical humid (3670)		167	Luzon Island (Philippines)	600	50	550	600	Klotzbücher et al. (2016)
Highly weathered soils									
Rain forest	Tropical humid (2100)	Ferralsol		Manaus (Brazil)	41	41	0	834	Lucas et al. (1993)
Rain forest	Tropical humid (2100)	Ferralsol		Manaus (Brazil)	51	51	0		Cornu (1995)
Rain forest	Tropical humid (1500)	Ferralsol		Mayombé (Congo)	58–76	58–76	0		Alexandre et al. (1997)
Campinarana	Tropical humid (2100)	Podzol		Manaus (Brazil)	21	21	0		Cornu et al. (1998)
Bamboo forest	Tropical humid	Podzol		Reunion Island	453–644	453–644	0		Meunier et al. (1999)
Rice	Subtropical warm humid (1676)		94	Northern Vietnam	600	110	490	230–370	Klotzbücher et al. (2016)
Rice	Subtropical warm humid (1676)		31	Northern Vietnam	360	90	270	150–210	Klotzbücher et al. (2016)
Rice	Subtropical warm humid (2840)		90	Northern Vietnam	280–390	50–60	230–330	280–390	Klotzbücher et al. (2016)
Rice	Tropical monsoonal (1930)		89	Southern Vietnam	370–470	90–140	280–330	170–240	Klotzbücher et al. (2016)
Rice	Tropical humid (3300)	Acrisol		Karnataka (South India)	234.3	0–189[b]	45.5–234.3		Prakash et al. (2011)
Rice	Tropical humid (3390)	Acrisol		Karnataka (South India)	129.5	0–108[b]	21.05–129.5		Prakash et al. (2011)
Rice	Subtropical warm humid (1680)	Acrisol		Northern Vietnam				107	Marxen et al. (2016)
Sugarcane	Tropical humid	Ferralsol		Mauritius Island	248				Ross et al. (1974)

[a] Total reserve in bases.

[b] 0 is the value if straws are not return on soil.

the topsoils of Ferralsols. Cornu (1995), Cornu et al. (1998), and Lucas et al. (1993) studied the Si cycle in neighboring forests on a Ferralsol and a Podzol. In both soils (Table 2), the biological pumping and subsequent biocycling of Si were crucial since plants took up Si in deep soil horizons and returned it to the topsoil, where DSi governed clay formation. In the Ferralsol, the availability of Al and Si promoted the formation of kaolinite whereas in the Podzol, the leaching of Al as mobile Al-humus complex led to a relative accumulation of residual quartz. Meunier et al. (1999) measured an exceptional Si uptake in a bamboo forest (*Nastus borbonicus*, high Si-accumulating) that developed on a Podzol overlying a strongly weathered Andosol. The Si biocycling was so active that the bamboo forest recycled huge quantities of phytoliths that accumulate in soil to eventually build up a bleached phytolithic E horizon over a spodic Bhs horizon. In this case, the loop was partial because of soil phytoliths accumulation (Meunier et al., 1999).

5. The impact of agricultural land use on the Si soil-plant cycle

Agricultural practices impact the silicon cycle through (i) harvesting plant parts that contain phytoliths (Guntzer et al., 2012; Vandevenne et al., 2011), (ii) changing soil pH (Fraysse et al., 2006; Guntzer et al., 2012; Haynes and Zhou, 2018), (iii) promoting erosion (Clymans et al., 2015), (iv) using silicate amendments (e.g. Haynes and Zhou, 2018; Ross et al., 1974; Savant et al., 1996, 1999), (v) altering soil aggregates through tillage practices (Li, 2019). Agriculture especially impacts the silicon soil-plant cycle since the five most cultivated crops - sugarcane, maize, rice, wheat, and barley - (ranked by mass produced globally, FAO, 2018) are high-Si-accumulating plant species. Carey and Fulweiler (2012) assessed that the total BSi produced in cultivated lands was 29.4 Tmol yr^{-1} namely 35% of total BSi produced annually by terrestrial plants (84 ± 29 Tmol $year^{-1}$ globally). In the humid tropics, sugarcane and rice, which are particularly efficient in Si accumulation, are the two main cultivated crops.

5.1. Plant Si uptake is largest in croplands established on slightly weathered soils

In slightly weathered soils, plant available DSi is constrained by the reserve of LSi minerals (Figs. 2 and 3). High Si-accumulating plants (e.g. rice, sugarcane or banana) take up very large amounts of Si ranging from 218 to 1470 kg ha^{-1} yr^{-1} (Henriet et al., 2008a,b; Klotzbücher et al., 2015b, 2016; Yang and Zhang, 2018) (Tables 2 and 3). Here, the management of non-edible plant parts is crucial as it largely influences the soil-plant Si cycle (Klotzbücher et al., 2015b; Savant et al., 1996, 1999). Rice straws are often removed from the field in South and Southeast Asia, where most of the rice is grown worldwide, for various purposes such as animal fodder, fuel for stoves, or burning (Savant et al., 1996; Seyfferth et al., 2013). As rice straws contain about 86% of total plant Si (Klotzbücher et al., 2015a), their removal strongly influences the soil-plant Si cycle by disrupting the biological silicon feedback loop and therefore enhancing soil desilication (Seyfferth et al., 2013) and LSi/PSi weathering (Yang and Zhang, 2018). The harvest of sugarcane generally involves the export of the stalks while the leaves return to soil either green or burned. As stalks contain about 15–20% of the total plant Si (Ayres, 1966; Kingston, 2008), little Si amount is usually exported in sugarcane croplands. In slightly weathered soils, the biological Si feedback loop is thus very active if high Si-accumulating plants are used, and if non-edible plant parts return to soil.

5.2. Plant Si uptake is lowest in croplands established on highly weathered soils

In highly weathered, desilicated soils, the pool of bioavailable Si is low. The annual Si uptake by rice plant varies between 129.5 and 600 kg ha^{-1} yr^{-1} (Table 2) (Klotzbücher et al., 2016; Prakash et al., 2011). These values are relatively low (Henriet et al., 2008a,b; Klotzbücher et al., 2015b; Miles et al., 2014) compared to Si uptake by plants cropped on slightly weathered soils (Tables 2 and 3, Fig. 4b). Si is thus considered as "deficient" in highly weathered soils. Si supply has a positive impact on sugarcane and rice crop yields through Si fertilizers (Allorerung, 1989; Ayres, 1966; D'Hotman and Villiers, 1961; Foy, 1992; Kawaguchi, 1966; Klotzbücher et al., 2018; Ross et al., 1974; Savant et al., 1996, 1999; Takijima and Gunawardena, 1969) as well as phytolithic biochar (Li et al., 2018).

5.3. Land use change impacts hydrology and related Si fluxes

Land use changes greatly impact the hydrology of the soil-plant system (Carlson and Traci Arthur, 2000; Davidson et al., 2012; Kosmas et al., 1997; Piao et al., 2007; Sanchez, 2019), in particular in the tropics (Piao et al., 2007; Sanchez, 2019). Deep rooting of trees in tropical evergreen forests allows to pump deep soil water, and limit

Table 3
Plant Si content in rice, banana, and sugarcane from different cultivated plots established on soils differing in weathering stage. The mean Si concentration is generally larger in the slightly weathered soils than in the highly weathered soils, but some values do not follow this trend.

Plant	Soil type	Plant part	Si %	Reference
Weakly weathered soils				
Rice	Vertisol	Plant composite	3.4–3.61	Tavakkoli et al. (2011)
Rice	Cambisol	Straw	3.051	Yang and Zhang (2018)
Rice	Cambisol, Luvisol, and Nitosol	Straw	7.6–9.1	Klotzbücher et al. (2016)
Rice	Cambisol, Nitisol, and Vertisol	Straw	6.3–8.1	Klotzbücher et al. (2016)
Rice	Nitosol, and Acrisol	Straw	7.6	Klotzbücher et al. (2016)
Banana	Andosol	Leaf	1.3	Henriet et al. (2008b)
Banana	Cambisol	Leaf	1.2	Henriet et al. (2008b)
Highly weathered soils				
Rice	Acrisol	Straw	5.4	Marxen et al. (2016)
Rice	Gleysol	Straw	4-4.1	Klotzbücher et al. (2016)
Rice	Acrisol	Straw	4-4.3	Klotzbücher et al. (2016)
Rice	Acrisol	Straw	4.4-4.8	Klotzbücher et al. (2016)
Rice	Gleysol, and Fluvisol	Straw	2.8–3.2	Klotzbücher et al. (2016)
Rice	Acrisol	Straw	2.6	Prakash et al. (2011)
Rice	Acrisol	Straw	1.53	Prakash et al. (2011)
Rice	Ferralsol	Plant composite	0.24–0.42	Tavakkoli et al. (2011)
Sugarcane	Ferralsol	Leaf	0.42-0.61	Ross et al. (1974)
Sugarcane	Ferralsol	Plant composite	0.7	Rodrigues (1997)
Banana	Nitisol	Leaf	0.75	Henriet et al. (2008b)
Banana	Ferralsol	Leaf	0.56	Henriet et al. (2008b)

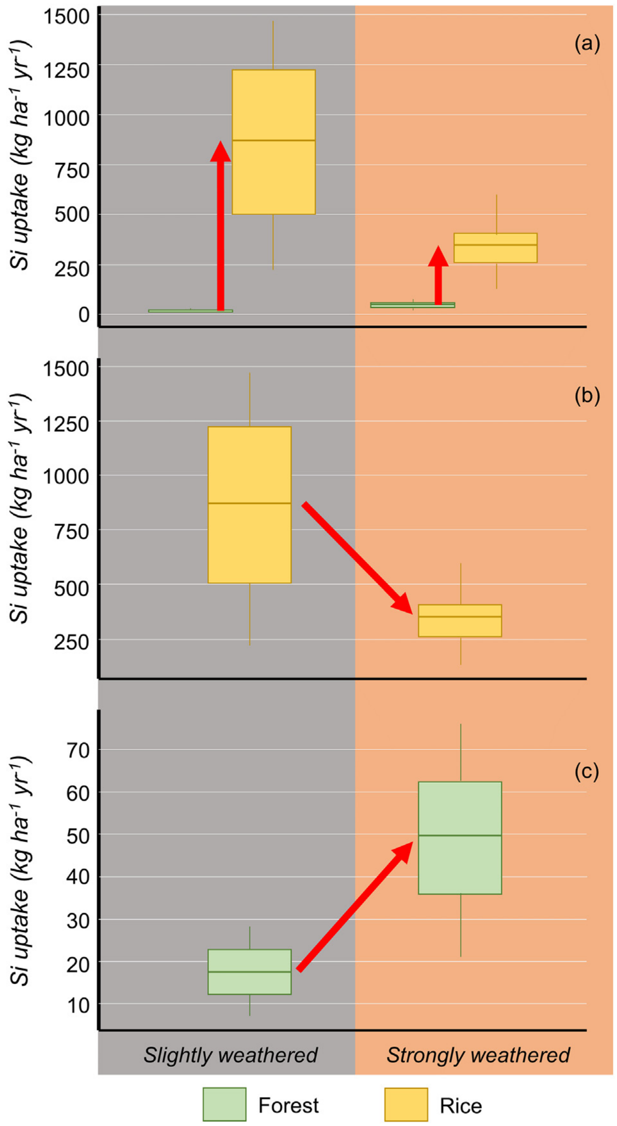

Fig. 4. Annual Si uptake values for (a) natural forest ecosystems and rice crops, (b) rice crops, and (c) natural forests, established on soils that are slightly (left) or strongly (right) weathered in the humid tropics. The figures from Table 2 (excluding bamboo and sugarcane) were computed with the ggplot function of the R programming language. The graph (a) allows comparison between forest and rice cropping. Graph (b) compares slightly and highly weathered soils for rice crop. Graph (c) compares slightly and highly weathered soils for natural forest ecosystems. Boxes extent represents the values from the first quartile to the third quartile. The line cutting the box is the median. The vertical lines (whiskers) represent the range of values. From (a) we note that rice crop has always larger Si uptake than forest. From (b) we observe that Si uptake by rice plant decreases when soil desilication increases. From (c) we conclude that Si uptake by forest plants increases with increasing soil weathering.

water losses (Nepstad et al., 1994, 2004). Moreover, the very large leaf area index of evergreen forest's canopy increases rainfall interception, limiting water losses from the soil-plant system by runoff and infiltration (Bruijnzeel and Sampurno, 1990; Sanchez, 2019).

Converting forest into cropland drastically decreases rooting depth, hence deep soil exploration by roots (Canadell et al., 1996; Jackson et al., 1996; Kleidon and Heimann, 1998), and leaf area index (Sanchez, 2019). This leads to substantial decreases in evapotranspiration and water interception by canopy, hence increasing water losses through runoff and infiltration (Davidson et al., 2012; Piao et al., 2007; Sanchez, 2019). In addition, soil compaction resulting from tillage practices can lead to increased runoff. Finally, irrigation practices in croplands may constitute significant additional water and nutrients inputs, especially for flooded rice (Desplanques et al., 2006; Klotzbücher et al., 2015b; Riotte et al., 2018a).

We distinguish here Si inputs to soil from rainfall and irrigation, and Si output by leaching and runoff (Table 4). They are controlled by water fluxes and associated Si concentrations.

5.3.1. *Si input from rainfall*

Si concentrations in rainfall waters are generally very low (Alexandre et al., 1997; Klotzbücher et al., 2015b; Meunier et al., 2010; Riotte et al., 2018a), leading to negligible Si inputs by rainfall (Table 4) (Alexandre et al., 1997; Meunier et al., 2010).

5.3.2. *Si input from irrigation*

While absent in forests, Si input can be large in flooded rice croplands (Desplanques et al., 2006; Klotzbücher et al., 2015b; Riotte et al., 2018a), in which it depends on irrigation dose and frequency (Klotzbücher et al., 2015b) (Table 4). It may also depend on the reserve of weatherable minerals in the catchment area upstream of the irrigated perimeters, since it strongly impacts DSi concentration in rivers downstream (see Cornelis et al., 2011 for a review). Unfortunately, to the best of our knowledge, no experimental data for flooded/irrigated rice croplands are available in highly weathered soils of the humid tropics to test this hypothesis. Riotte et al. (2018a) measured irrigation inputs of Si in moderately weathered soils under a tropical savanna climate (Koppen classification, Mean Annual Rainfall 970 mm), i.e. not in the humid tropics. Si irrigation input amounted to 153 kg Si ha^{-1} season^{-1} (Riotte et al., 2018a), which is similar to the values reported by Klotzbücher et al. (2015b) in weakly weathered soils under monsoon climate.

5.3.3. *Increase in Si release upon flooding*

Such an increase was reported in pot and field experiments under rice cropping (Ma and Takahashi, 1989; Marxen et al., 2016), likely on moderately weathered soils. In the study conducted by Marxen et al. (2016), redox potential rapidly decreased to ~ − 160 mV within the first 6 days after flooding. Actually, flooding induces reduction reactions, which involve electron exchange and proton (H^+) consumption, thus inducing pH increase. Regardless of their original pH, most soils reach pH values of 6.5–7.2 rapidly after flooding and remain at that level while submerged: the increase in pH in flooded acid soils may reach 3 pH units in a week (Ponnamperuma, 1972; Sanchez, 2019). Such a pH increase undoubtedly reduces mineral weathering, and thus limits the release of Si from LSi and/or PSi mineral dissolution whereas it may considerably enhance phytolith dissolution in solution (Fraysse et al., 2009) and soil (Li et al., 2019). The impact of flooding on the coupled increase in pH and Si release from phytolith is, however, unknown, despite its importance on Si fluxes in paddy fields.

5.3.4. *Si outputs by leaching or runoff*

Si output by leaching or runoff tends to increase when converting forest into rice cropland in weakly weathered soils, except for one very low Si output value due to soil impermeability (Klotzbücher et al., 2015b). Using hydrological modelling, Nguyen et al. (2016) attributed an exceptionally high leachate output of Si (10,000 kg Si ha^{-1} yr^{-1} (Table 4)) to high water infiltration rate in soil. In contrast, in natural forests on highly weathered soils, leachate outputs of Si were relatively low (4–26 kg Si ha^{-1} yr^{-1}), and in the same range as the value reported by Meunier et al. (2010) for a forest on a little weathered soil. Thus, available literature data do not allow us to infer about the impact of soil weathering stage on Si output through leaching. As far as land use is concerned, literature data suggest that leachate output of Si should be limited in forests regardless of soil weathering stage, whereas data for rice croplands in highly weathered soils are missing. We therefore hypothesize that Si output through leaching from highly weathered soils is below that in weakly weathered soils since DSi concentration in soil

Table 4

Experimental values of Si input by rainfall, Si input by irrigation, and Si output by leaching or lateral flow in various forest and agricultural ecosystems.

Ecosystem	Climate (MAP in mm)	Soil weathering degree		Location	Si input by rainfall ($kg\ ha^{-1}\ yr^{-1}$)	Si input by irrigation ($kg\ ha^{-1}\ yr^{-1}$)[a]	Si output by leaching or lateral flow ($kg\ ha^{-1}\ yr^{-1}$)	Reference
		WRB class	TRB					
Weakly weathered soils								
Rain forest	Tropical humid (4200)	Leptosol		Reunion Island	1.9	0	15	Meunier et al. (2010)
Rice	Monsoon tropical (2050)		168	Luzon Island (Philippines)	0	78[b]	274	Klotzbücher et al. (2015b)
Rice	Monsoon tropical (2050)		168	Luzon Island (Philippines)	0	100[c]	3	Klotzbücher et al. (2015b)
Rice	Monsoon tropical (2050)		168	Luzon Island (Philippines)	0	644[d]	805	Klotzbücher et al. (2015b)
Rice	Tropical humid (> 1600)	Fluvisols		Northern Vietnam	nd	nd	10,000	Nguyen et al. (2016)
Highly weathered soils								
Rain forest	Tropical humid (2100)	Ferralsol		Manaus (Brazil)	nd	0	11	Lucas et al. (1993)
Rain forest	Tropical humid (2100)	Ferralsol		Manaus (Brazil)	nd	0	26	Cornu (1995)
Rain forest	Tropical humid (1500)	Ferralsol		Mayombé (Congo)	1	0	16	Alexandre et al. (1997)
Campinarana	Tropical humid (2100)	Podzol		Manaus (Brazil)	nd	0	4.5	Cornu et al. (1998)
Dry deciduous forest	Tropical subhumid (1100)	Ferralsol		Southern India	nd	0	19.8	Riotte et al. (2018b)

[a] Includes DSi and ASi inputs.

[b] Water input by irrigation is $221\ l\ m^{-2}$.

[c] Water input by irrigation is $140\ l\ m^{-2}$.

[d] Water input by irrigation is $2006\ l\ m^{-2}$.

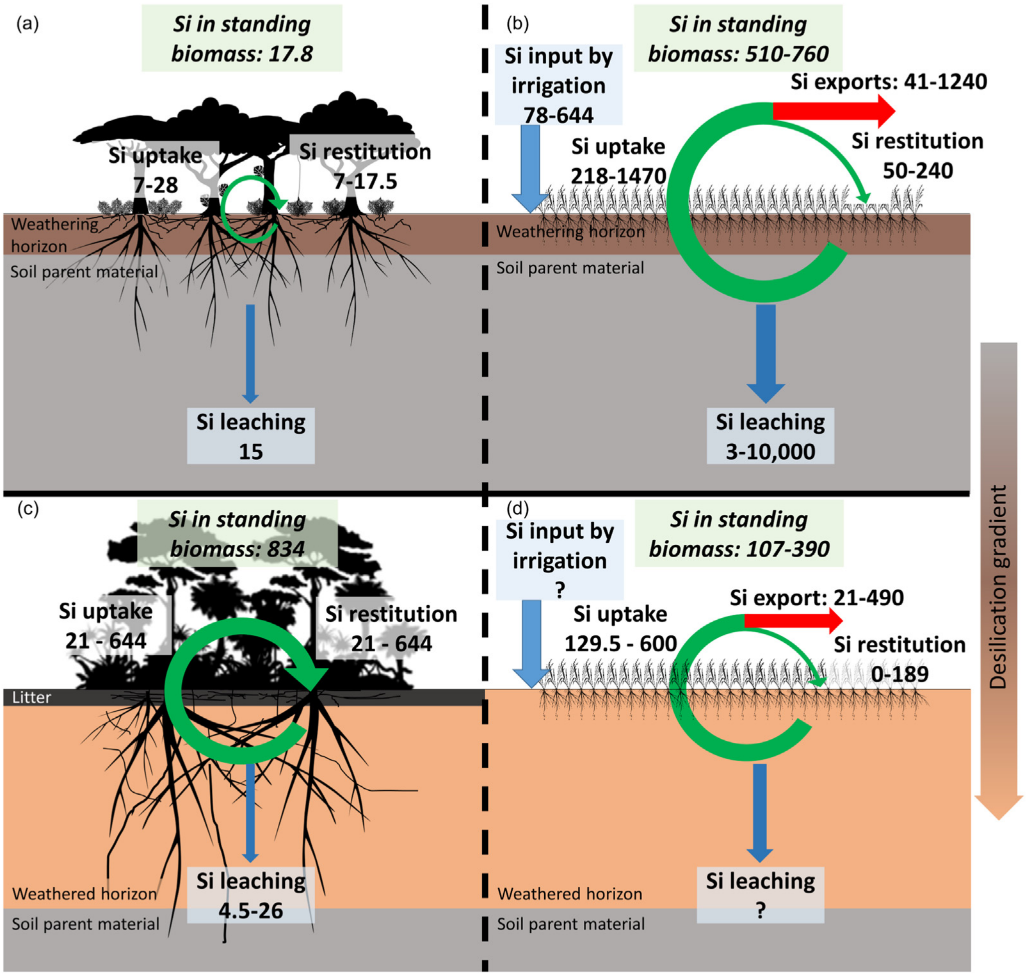

Fig. 5. Schematic view of the soil-plant cycle of Si under forest (a, c) and rice crop (b, d). (a) and (b) concern the biocycling of Si in less weathered soils. (c) and (d) concern the bio-cycling of Si in highly weathered soils. All figures refer to annual Si fluxes except the values in *italics*, which refer to reservoirs. Little weathered soil horizons are in grey color while the strongly weathered/desilicated ones are in orange. Soil horizons at intermediate stage of weathering are in brown. In slightly weathered soils, the biocycling of Si is lower in forests than in rice cropland. In highly weathered soils, the biocycling of Si is comparable between forest and rice fields, but Si restitution to soil may be importantly lowered by straw exports out of rice fields. Si in standing biomass evolves in the following order: Forest on highly weathered soil > Rice on slightly weathered soil > Rice on highly weathered soil > Forest on slightly weathered soil. In natural ecosystems, the biocycling of Si is larger for strongly weathered soils while in croplands, the biocycling of Si is larger for slightly weathered soils. References are given in Tables 2 and 4. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

solution decreases with increasing soil weathering stage in cultivated ecosystems (Henriet et al., 2008a,b; Klotzbücher et al., 2015a; Makabe et al., 2009).

6. Soil weathering stage affects the soil-plant cycle of silicon, but depending on land use

Fig. 4 illustrates graphically the Si plant uptake data presented in Table 2 for forest and rice crop, excluding other crops (mainly sugarcane) and bamboo forest: the former are too scarce to draw conclusions, the latter is an exceptional case (Meunier et al., 1999). Si plant uptake is always larger for rice crop than for natural forest (Fig. 4a), the difference being particularly important on slightly weathered soils. With increasing soil weathering stage, the Si uptake decreases for rice crop (Fig. 4b) whereas it increases for natural forest (Fig. 4c).

These facts are illustrated in Fig. 5, which provides a schematic view of the biological Si feedback loop. *On slightly weathered soils*, this loop involves much lesser amounts of Si under forest than rice crop established (Fig. 5a–b). This much less intense loop is likely because the forest ecosystem shelters few high Si-accumulating plants whereas rice is a high Si-accumulator. Besides, cropping stimulates plant growth and development through fertilizer use and plant protection techniques whereas N and P generally limit the primary production of forest developing on slightly weathered soils (Laliberté et al., 2013). The biological Si feedback loop under rice farming is thus stimulated because of increasing plant growth. *In highly weathered soils*, the biological Si feedback loop is comparable between forest stands and rice croplands, but Si restitutions may be importantly lowered by rice straw exports. A very interesting fact is that soil desilication involves an increase of the biological feedback loop of Si in forests, but a reduction of this loop in cropland. This discrepancy is likely due to the following factors: (i) readily soluble phytoliths make the pool of plant available Si; (ii) forest litter is densely explored by fine roots pumping mineral elements; (iii) deep rooting of forest trees enhances mineral pumping and limits the leaching of dissolved Si; (iv) crop harvesting exports Si out of cultivated ecosystems. Humid tropical forest is one of the biomes with the deepest rooting depth and largest root biomass (Canadell et al., 1996; Jackson et al., 1995, 1996; Kleidon and Heimann, 1998; Nepstad et al., 2004; Schenk and Jackson, 2002, 2005). In contrast, cropland is one of the biomes with the shallowest rooting depth and lowest root biomass (Canadell et al., 1996; Jackson et al., 1996; Kleidon and Heimann, 1998). Maximum rooting depth and root biomass for tropical evergreen forests are 7.3 ± 2.8 m (Canadell et al., 1996) and 5 kg m^{-2} (Jackson et al., 1996), respectively; while they are 2.1 ± 0.2 m (Canadell et al., 1996) and < 1.5 kg m^{-2} (Jackson et al., 1996), respectively, for croplands. For rice plants, 82% to 99% of the roots are located in the first 30 cm of the soil (Yoshida and Hasegawa, 1982). For tropical evergreen forests, 69% of the roots are in the first 30 cm of the soil. In forest ecosystems, tree roots are deep enough to absorb nutrients from deep and slightly weathered horizons (Jobbágy and Jackson, 2001; Lucas et al., 1993). Moreover, in the forest ecosystem, the litter forms an environment with a very dense root network in which limiting nutrients are concentrated (Jobbágy and Jackson, 2001), the turnover of C and nutrient cycling is large (Greenland and Nye, 1959), and the dissolution of phytoliths is rapid (Fraysse et al., 2010). This strongly minimizes the loss of elements by leaching (see Section 5.3) (Lucas et al., 1993), which explains why such weathered soils support evergreen forests with the greatest biodiversity and biomass (Beer et al., 2010; Laliberté et al., 2013; Myers, 1988). Two Si sinks thus occur in natural forest ecosystems while they strongly decrease in croplands: the subsoil LSi pool that is exploited by the deep roots of forest trees; the topsoil PhSi pool that is directly exploited by a very dense root network.

In cropping systems established on highly weathered soils, Si management is thus crucial to substantially increase crop yields in a sustainable way (a.o. Guntzer et al., 2012; Klotzbücher et al., 2015a,b, 2018; Li et al., 2019).

7. The impact of liming on the soil-plant Si cycle depends on soil weathering stage

Liming is a common agricultural practice that increases soil pH, depending on soil buffer capacity (Li et al., 2019). The impact of the increase in soil pH on the soil-plant Si cycle is still unclear. Increasing pH either decreases the bioavailability of Si because of increasing Si adsorption (Berthelsen et al., 2003; Haynes and Zhou, 2018; Savant et al., 1999; Tavakkoli et al., 2011), or increases Si bioavailability (Camargo et al., 2007; Li et al., 2019; Mantovani et al., 2016; Miles et al., 2014). As a matter of fact, studies on the impact of liming on the Si soil-plant cycle are still scarce (Guntzer et al., 2012; Haynes and Zhou, 2018; Klotzbücher et al., 2018; Tavakkoli et al., 2011), despite soil pH can strongly control Si bio-availability (Meunier et al., 2018).

In humid tropical conditions, LSi and PSi minerals dissolve through acidic hydrolysis (Lindsay, 1979). Increasing soil pH by liming would therefore limit the dissolution of these silicates since the added alkaline agent becomes the privileged consumer of protons. In contrast, increasing soil pH by liming would increase the dissolution of phytoliths (Fraysse et al., 2006, 2009, 2010; Klotzbücher et al., 2018). Besides, increasing soil pH may promote the deprotonation of $H_4SiO_4^0$ but only at very high pH value since it is a very weak acid ($pK_a = 9.8$), and deprotonation may theoretically favor Si adsorption onto Al and Fe oxides (Haynes and Zhou, 2018; Tavakkoli et al., 2011). The impact of liming on the soil-plant Si cycle depends on four factors: (i) soil buffering capacity, (ii) the reserve of LSi and PSi minerals, (iii) the PhSi pool, and (iv) the pool of secondary Al and Fe oxides; that are all impacted by soil weathering stage. Soil weathering stage may thus influence the impact of liming on the soil-plant Si cycle. However, increasing soil pH may decrease the magnitude of positive charges born by Fe and Al oxides, and thus decrease Si adsorption (Uehara and Gillman, 1981). Considering all the factors influenced by liming that control the Si bioavailability (soil buffer capacity, the reserve in LSi, PSi, PhSi, and secondary Al and Fe oxides), it is extremely complex to predict the impact of liming on the soil-plant Si cycle. Especially for highly weathered soils, whose composition varies greatly depending on the parent material, and the management of non-edible plant parts at harvest.

Another alternative is to amend soil with Si fertilizers such as a.o. blast furnace slag (Haynes and Zhou, 2018), ground basalt (Beerling et al., 2018; Haynes and Zhou, 2018), or phytolith-rich biochar (Li et al., 2018; Li et al., 2019). A concomitant increase in soil pH and bioavailable Si pool was observed following application to soils of slags (Camargo et al., 2007; Haynes and Zhou, 2018; Mantovani et al., 2016) and phytolith-rich biochar (Li et al., 2019).

8. The transition from forest to rice crop – the Q-I relationship

From all these observations, the Si quantity-intensity relationship can be redrawn for rice cropping systems (Fig. 6). In slightly weathered soils, converting forest areas into rice croplands results in enhancing the weathering of LSi because of the large uptake of Si by rice (Yang and Zhang, 2018). The LSi pool therefore decreases. The PhSi pool strongly depends on the management of rice straws (Klotzbücher et al., 2015b, 2016; Marxen et al., 2016; Seyfferth et al., 2013). In highly weathered soils, that conversion likely leads to the decrease in the PhSi pool if rice straws are exported out of the field (Klotzbücher et al., 2015b, 2016; Marxen et al., 2016; Seyfferth et al., 2013). In this case, the activity of $H_4SiO_4^0$ could rapidly drop since the LSi pool is exhausted and can no longer maintain high $H_4SiO_4^0$ concentrations. Finally, Si fertilizer use (Fig. 6(5)) would increase the $H_4SiO_4^0$ activity from *d* to *f* in Fig. 6 (Haynes and Zhou, 2018). In this case, the PhSi pool could slightly increase if straws are not exported as the plant uptake of Si increases (Savant et al., 1996, 1999).

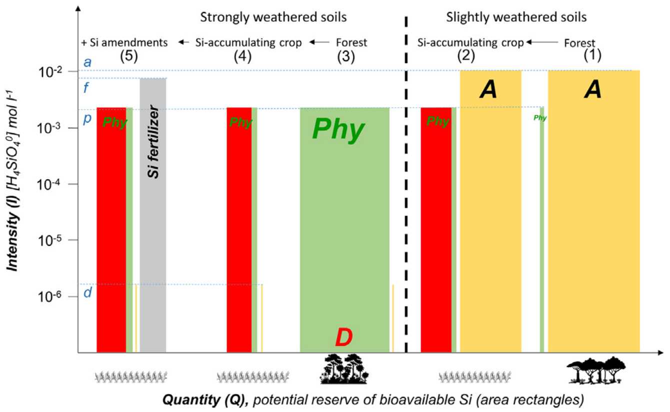

Fig. 6. Si quantity-intensity (Q-I) relationship under forest and rice field in slightly and highly weathered soils. In slightly weathered soils, converting forest (1) to rice cropland (2) decreases the LSi pool through mineral weathering, which is accelerated because of large Si uptake by rice. The PhSi pool depends on the management of rice straws (the red area corresponds to the potential PhSi pool if rice straws are restituted to soil). In highly weathered soils, converting forest area (3) into rice cropland (4) decreases the PhSi pool. The export of rice straws strongly influences the PhSi pool (red area). If rice straws are exported from the field, the activity of $H_4SiO_4^0$ would abruptly drop from *p* to *d* level. Eventually, when Si fertilizers are used (5), a new Si pool (grey area) is created and increases the $H_4SiO_4^0$ activity from *d* to *f*. The PhSi pool could therefore slightly increase if straws are not exported as plant Si uptake increases. The size of each rectangle represents the related Si stock. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

9. Conclusion

The biological silicon feedback loop strongly differs between natural and cultivated environments in the humid tropics. Soil weathering stage has an opposite impact on the biological silicon feedback loop in natural and cultivated environments. In the former environments, the increase in soil weathering stage tends to raise the importance of the biological silicon feedback loop at the expense of the mineral contribution. In cultivated environments, an increase in soil weathering stage leads to a decrease in Si biocycling. The conversion of forest into cropland has thus a tremendous impact on the Si soil-plant cycle. The differences between forest area and cropland are attributed to very different rooting depths, litter composition, soil cover, recycling or export of plant parts, density of high Si-accumulating plant species, soil and soil fertility management. Until now, studies on the Si cycle in cultivated ecosystems in the tropics have mostly focused on rice and sugarcane, two high Si-accumulating plant species. Furthermore, our conclusions are only based on the few studies available so far for rice croplands and forest ecosystems in weakly and highly weathered soils in the humid tropics. We expect that the impact of the agricultural land use on the Si cycle would largely differ for non Si-accumulating plants. Further studies are needed to understand deeper the impact of agricultural land use on the Si soil-plant cycle. Taking soil weathering stage into account seems, however, very important to understand the impact of agricultural land use on the Si cycle.

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