Plant Soil (2008) 313:71–82
DOI 10.1007/s11104-008-9680-7

REGULAR ARTICLE

Leaf silicon content in banana (*Musa* spp.) reveals the weathering stage of volcanic ash soils in Guadeloupe

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Received: 3 March 2008 / Accepted: 4 June 2008 / Published online: 26 June 2008

Abstract Several plant species accumulate silicon, which is taken up by roots in soil solution. The Si concentration in soil solution can be governed by silicate dissolution and formation, and thus soil constitution. Here, we study the Si leaf content of mature banana plants (*Musa acuminata* cv Grande Naine) cropped on soils derived from andesitic ash in Guadeloupe through standard foliar analysis. The soils strongly differ in weathering stage and total Si content. The most desilicated soils (Andosol–Nitisol–Ferralsol) occur in the wettest areas, on the Eastern slopes (Es) of the volcano exposed to rain bearing winds. Least weathered soils (Andosol–Cambisol) occur on Western slopes (Ws). The average leaf Si concentration ranges from 2.7 to 3.9 g kg^{-1} for bananas cropped in Es soils, and from 7.7 to 9.6 g kg^{-1} in Ws soils. The leaf Si concentrations are lowest for the Es gibbsite-rich Andosols and Ferralsols. The leaf Si concentration is positively correlated with soil $CaCl_2$-extractable Si content, soil Si content and total reserve in weatherable minerals. The silicon content of banana leaves thus reveals the weathering stage of volcanic ash soils in Guadeloupe.

Keywords Silicon · *Musa* · Foliar diagnosis · Soil weathering · Transpiration

Responsible Editor: Jian Feng Ma.

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Introduction

Silicon plays a crucial role in global biogeochemical processes such as the regulation of carbon dioxide (Berner 1995; Kump et al. 2000), the buffering of proton fluxes through silicate dissolution (Rai and Kittrick 1989), and the nutrition of both marine and terrestrial biota (Smetacek 1999). Since the rates of mineral dissolution can be enhanced by plant impact on silicate weathering (Moulton et al. 2000), plants can exert a strong imprint on the Si continental cycle, and thereby on Si release to water streams (Derry et al. 2005). Several plant species readily accumulate silicon, which is, however, not considered as an essential plant nutrient (Epstein 1994). Si-accumulators are mostly monocots (Ma and Takahashi 2002).

Silicon is taken up by plant roots in the form of water-soluble H_4SiO_4 and follows the water flow from roots to transpiration sites (Raven 2001) through passive and active transport (Ma et al. 2006). Therein, silica precipitates within particles of biogenic opal ($SiO_2 \cdot nH_2O$), called phytoliths (Smithson 1956). In controlled conditions, the supply of H_4SiO_4 in the nutrient solution governs the content of Si in plant tissue (Van der Vorm 1980; Henriet et al. 2006).

Silicon soil-to-plant transfer could thus be influenced by the availability of aqueous H_4SiO_4 in soil, and by the plant transpiration rate. The concentration of H_4SiO_4 in soil solution may range between 0.01 and 1.99 mM (Karathanasis 2002). It varies depending on Si plant uptake, adsorption onto Fe- and Al-oxides, silicate weathering and dissolution, and silicate formation (Sommer et al. 2006). The mineralogical constitution of soils may thus control the concentration levels of H_4SiO_4 in the soil solution (Kittrick 1969; Karathanasis 2002). In humid tropical regions, desilication is a major trait of weathering (Chadwick et al. 2003). In these areas, weathering sequences of soils developed on volcanic ash are remarkably suited to study the impact of soil weathering stage on soil constitution and properties (Parfitt et al. 1983; Delvaux et al. 1989; Chadwick et al. 2003), on plant nutrient status (Delvaux et al. 1989; Chadwick et al. 1999), and likely on plant Si concentration (Fox et al. 1967).

Silicon accumulation by young banana plantlets (*Musa acuminata* cv Grande Naine) in hydroponics is controlled by the concentration of Si in the nutrient solution (Henriet et al. 2006). Here, we assess the silicon status of mature banana plants cropped on soils developed on andesitic ash, but differing in their weathering stage and mineralogical constitution (Colmet-Daage and Gautheyrou 1974; Ndayiragije 1996; Ndayiragije and Delvaux 2004). We further evaluate the availability of Si for plants in these soils, and infer its dependence on soil constitution and weathering stage.

Environmental framework

In the island of Basse-Terre, Guadeloupe (16° N, 61° W), Caribbean area, volcanic ash soils cover extensive areas on the surrounding slopes of the active volcano La Soufrière (1,467 m asl), and of eroded ancient volcanoes active during Tertiary times (Colmet-Daage and Lagache 1965). The ash deposits of Quaternary and Pliocene times are of andesitic composition; plagioclase, pyroxene and ferromagnesian volcanic glasses are the dominant weatherable minerals (Dagain et al. 1981; Ndayiragije 1996). The ashy materials readily weathered under humid tropical conditions. On the Western slopes (Ws) of the volcano, the Ws soil pattern involves an Andosol–Cambisol–Vertisol toposequence from 500 m asl to sea level, corresponding to mean annual rainfall (MAR) decreasing from ~3,500 to ~1,000 mm (Fig. 1), and to the mineralogical sequence ash → allophane → halloysite/smectite → smectite (Colmet-Daage and Lagache 1965; Pineros Garcet 1994). The Eastern slopes (Es) of the volcano are exposed to rain-bearing winds from the Atlantic Ocean: MAR exceeds 5,000 mm at 500 m asl, and decreases to 2,500 mm downslope at sea level (Fig. 1). The Es soil pattern involves an Andosol–Nitisol–Ferralsol weathering sequence, corresponding to the mineralogical sequence ash → gibbsite, allophane → halloysite, Fe-oxide → kaolinite, Fe-oxide, gibbsite (Colmet-Daage and Lagache 1965; Ndayiragije 1996; Ndayiragije and Delvaux 2003, 2004). Ws Andosols and Cambisols as well as Es Andosols, Nitisols and Ferralsols have long been extensively used for intensive banana cropping (Colmet-Daage and Lagache 1965; Ndayiragije 1996; Dorel et al. 2000). The soils are thus fertilized, notably by K, Ca, and Mg supplies.

Materials and methods

Experimental sites and general sampling scheme

Six experimental sites were selected on the basis of the detailed 1:20,000 soil map of Guadeloupe (Colmet-Daage 1969; Fig. 1). Their main characteristics are presented in Table 1. Two sites corresponded to the Ws Andosols (Ws-An) and Cambisols (Ws-Ca), and four sites to the Es perhydrated Andosols (Es-An1), Andosols (An2), Nitisols (Es-Ni), and Ferralsols (Es-Fe). The Ferralsols (Es-Fe) developed from Tertiary pyroclasts deposited during Pliocen (Dagain et al. 1981). The other soils developed from Quaternary ash deposits (4,000–140,000 years BP) (Colmet-Daage and Gautheyrou 1974; Dagain et al. 1981). They are members of chronotoposequences characterized by decreasing elevation and decreasing MAR in the order Ws-An–Ws-Ca on western slopes, and Es-An1–Es-An2–Es-Ni on eastern slopes (Fig. 1).

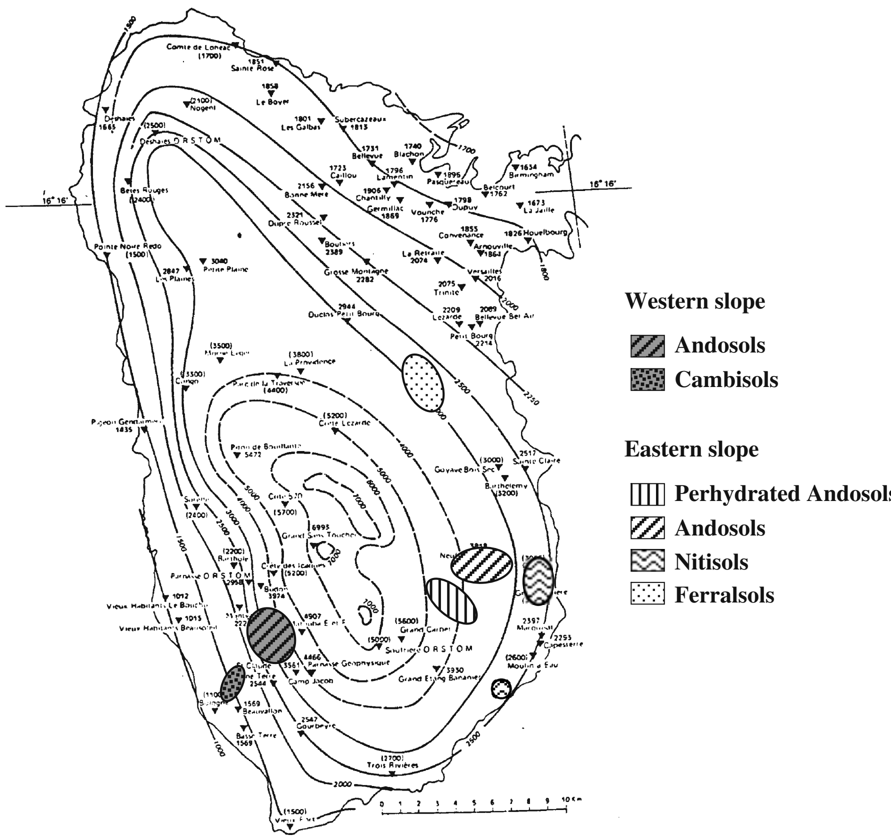

Fig. 1 Mean annual rainfall (mm) map of the island Basse-Terre (Guadeloupe) (Chaperon et al. 1985). *Circles* indicate the localization of the experimental sites on each major soil type: Andosol, Cambisol, Nitisol, Ferralsol, of the Western and the Eastern slopes of the volcano La Soufrière

In each experimental site, we selected ten cultivated banana plots. The cultivar was *Musa acuminata* cv Grande Naine (group AAA, Cavendish, dessert banana). In each plot, we selected ten plants of similar crop yield potential, i.e. homogeneous pseudostem circumference (~65–70 cm as measured for each plant at 1 m from soil surface), at flowering. For each plant, we sampled the external part of the lamina at the centre (100 mm width) of the antepenultimate leaf (leaf III), following the international standard set up for banana foliar diagnosis (Martin-Prével 1980). The ten foliar samples were mixed up as a composite leaf sample for

Table 1 Some characteristics of the six experimental sites corresponding to the Western (Ws) and Eastern (Es) slopes of the volcano La Soufrière

Symbol	Soil type (WRB: ISSS 1998)	Locality	Elevation[a] (m asl)	Rainfall[b] (mm)	Clay minerals[c]
Ws-An	Humic Andosol	Grand-Val	471	3,448	Allophane
Ws-Ca	Haplic Cambisol	Belle-Vue	202	1,808	Halloysite, smectite
Es-An1	Molli-silicic Andosol	Féfé	412	4,697	Gibbsite, allophane, kaolinite, hydroxy-Al interlayered 2:1 minerals
Es-An2	Humic Andosol	Neufchâteau	226	3,645	Allophane, gibbsite, hydroxy-Al interlayered 2:1 minerals
Es-Ni	Haplic Nitisol	Changy	35	2,566	Halloysite, Fe oxide
Es-Fe	Haplic Ferralsol	Féneteau	162	3,284	Kaolinite, Fe oxide, gibbsite

[a] Average value of the sampling area

[b] Mean annual rainfall (Chaperon et al. 1985)

[c] Colmet-Daage and Lagache (1965); Colmet-Daage and Gautheyrou (1974); Pineros Garcet (1994); Ndayiragije (1996); Ndayiragije and Delvaux (2003, 2004)

each plot. We sampled the soil at 50 cm distance from the base of each of the ten banana plants selected for foliar sampling, by using a small auger calibrated at 00–20 cm depth. For each plot, the ten soil samples were mixed up as a composite bulk sample. The comprehensive sampling scheme thus involved 600 individual leaf and soil samples, leading to 60 composite plant and soil samples for further analyses.

The topsoil-foliar sampling was carried out between February and March 2006, after the period of plant growth during the rainy season (April to January). The coordinates and altitude levels were recorded at each plot with a global positioning system (Garmin®). The altitude levels were used to compute the mean annual rainfall (MAR) values for each plot according to the linear regressions established by Chaperon et al. (1985) for both the Western (Ws) and Eastern (Es) slopes of the volcano:

$$\text{Ws}: \quad \text{MAR(mm)} = 577 + 6.10 \times (\text{Elevation(m)})$$

$$r^2 = 0.97$$

$$\text{Es}: \quad \text{MAR(mm)} = 2,368 + 5.65 \times (\text{Elevation(m)})$$

$$r^2 = 0.94$$

Plant material and analysis

The 60 composite leaf samples were stored at 60°C for 1 week for dry weight determination. Mineral analysis was carried out after calcination at 450°C for 1 day and fusion in Li-metaborate + Li-tetraborate at 1,000°C (Chao and Sanzolone 1992), followed by ash dissolution with concentrated HNO_3. Nutrient and Si concentrations were measured by inductively coupled plasma-atomic emission spectrometry (ICP-AES).

Since the Si concentration shows a strong gradient between young and old leaves (Henriet et al. 2006), the foliar concentration of Si was also measured from leaf I to the oldest leaf. For this purpose, we selected a representative banana plot for each site, where soil conditions were close to the central concept of each site-specific soil. In each of these plots, we selected one banana plant among the ten selected for foliar diagnosis. The chosen plant had a pseudostem circumference closest to the average value at the plot level. For each plant, we sampled banana leaves from leaf I to the oldest leaf. All the procedure was then similar to the one described here above up to the determination of leaf Si concentration.

Soil material and analysis

The 60 bulk soil samples were moderately air-dried (12 h at room temperature, 20°C), sieved at 2 mm, and stored for further analyses. Sub-samples were dried at 105°C until constant weight to determine soil dry weight.

The $CaCl_2$-extractable Si content was determined in each bulk sample using 0.01 M $CaCl_2$ (adapted from Haysom and Chapman 1975). The extraction procedure was standardized as follows: a 5-g (equivalent dry weight) soil sample was placed into a 100 ml polyethylene cup with 50 ml extractant (soil/solution ratio 1:10) and shaken for 5 h at 20°C. The suspensions were then centrifuged at 3,400×g for 10 min, and the supernatants were filtered through Whatman no. 4 paper. The concentration of Si in the supernatant was determined by ICP-AES. The measurement of soil $CaCl_2$-extractable Si content was done twice. Soil pH was measured in H_2O in 5 g:25 ml suspensions. Cation exchange capacity (CEC) and the content of exchangeable cations were determined according to Jackson (1965). Elemental analysis was carried out for the 60 soil samples after calcination at 1,000°C and Li-metaborate + Li-tetraborate fusion (Chao and Sanzolone 1992). Briefly, a crushed sample of 100 mg was melted at 1,000°C for 5 min in a graphite crucible in the presence of 0.4 g Li-tetraborate and 1.6 g Li-metaborate. The cooled melt was then dissolved in 100 ml of 2 M HNO_3 under magnetic agitation at 100°C. The contents of elements (Si, Al, Fe, Ca, Mg, K, Na, Ti, and Mn) were determined by ICP-AES spectrometry. The total contents of alkaline and alkaline-earth cations were summed up as the total reserve in bases (TRB), which estimates the content of weatherable minerals in mineral soil horizons (Herbillon 1986).

Results

Soil properties

As illustrated in Table 2, the average pH values in each experimental site ranged between 5.1 and 6.0, denoting regular liming under intensive banana cropping (Ndayiragije 1996; Ndayiragije and Delvaux 2004). The average value of CEC significantly decreased from 57 to 22 $cmol_c\ kg^{-1}$ in the order Es-An1 > Es-An2 > Ws-An > Es-Ni > Ws-Ca = Es-Fe. The average contents of exchangeable Ca, Mg and K are relatively large, denoting the regular liming and fertilization practices in intensive banana cropping systems. The exchangeable Mg content was, however, significantly larger in Ws- than in Es-soils. The average value of ECEC decreased from 14.1 $cmol_c\ kg^{-1}$ in Ws-Ca to 7.8 $cmol_c\ kg^{-1}$ in Es-Fe. The exchange complex was desaturated in all soils except in the Cambisols Ws-Ca, where the average base saturation amounted to 63%.

The $CaCl_2$-extractable Si content in soils (mg kg^{-1}) varied from 8 in Es-An2 to 69 in Ws-Ca (data not shown). As shown in Table 2, the average $CaCl_2$-extractable Si content in soils significantly decreased from 54.3 to 18.7 mg kg^{-1} in the sequence Ws-Ca > Ws-An = Es-Ni > Es-Fe = Es-An1 = Es-An2, the largest values being measured in Ws-soils.

The TRB values decreased from 341 $cmol_c\ kg^{-1}$ in Ws-Ca (Cambisol) to 21 $cmol_c\ kg^{-1}$ in Es-Fe (Ferralsol) (data not shown). The total Si content in soils decreased from 269 g kg^{-1} in Ws-Ca (Cambisol) to 144 g kg^{-1} in the Es Andosols Es-An1 (data not shown). The average values of TRB and soil elemental contents in each experimental site are presented in Table 3. The average total Mg, Ca, K and Na contents were larger in Ws than in most Es soils. The total reserve in bases (TRB) sums up the elemental contents of alkaline and alkaline-earth cations, including the cations occluded in minerals as well as those located on ion exchange sites. In this respect, TRB estimates the content of weatherable minerals in mineral soil horizons (Herbillon 1986). The average TRB significantly decreased from 270 to 26 $cmol_c\ kg^{-1}$ in the order Ws-Ca > Ws-An > Es-An1 > Es-An2 = Es-Ni > Es-Fe. Ca and Mg were the major cations in the TRB, but their proportion largely decreased in the strongly weathered Andosols, Nitisols and Ferralsols from the Eastern slopes (Es-An2, Es-Ni, Es-Fe). The average total Si content was significantly larger in Ws (241–262 g kg^{-1}) than in Es soils (158–193 g kg^{-1}). The lowest average Si contents (159–158 g kg^{-1}) occurred in the Andosols Es-An1 and Es-An2. The largest average Al, Fe, and Ti contents occurred in Es soils (104–137 g kg^{-1} for Al, 85–111 g kg^{-1} for Fe, and 6.6–9.4 g kg^{-1} for Ti), and the lowest in Ws soils (~90 for Al, ~70 g kg^{-1} for Fe, and ~5.3 g kg^{-1} for Ti). The average Mn content was larger in Es-Ni (3.1 g kg^{-1}) and Es-Fe (3.4 g kg^{-1}) than in any other soils.

Leaf Si and nutrient concentrations

The Si concentration in banana leaf samples (g kg^{-1} DM) varied from 1.7 in the Ferralsol Es-Fe to 12.0 in the Cambisol Ws-Ca (data not shown). As shown in Table 4, the average leaf Si concentrations per experimental site ranged between 2.73 to 9.64 g kg^{-1} DM, respectively in Es-Fe (Ferralsol) and Ws-Ca (Cambisol) samples. The average leaf Si concentrations were

Table 2 Average values of $CaCl_2$-extractable Si content, pH, exchangeable bases levels, cation exchange capacity (CEC) and effective CEC, as measured in the fine earth (<2 mm) of soil samples from the six experimental sites (ten plots per site)

Soil	pH (H_2O)	Exchangeable bases/$cmol_c\ kg^{-1}$				ECEC/$cmol_c\ kg^{-1}$	CEC/$cmol_c\ kg^{-1}$	BS/%	$CaCl_2$ extractable Si/mg kg^{-1}
		Ca	Mg	Na	K				
Ws-An	5.4±0.1	7.6±0.5	3.0±0.2	0.12±0.0	2.3±0.2	13.0±0.7	35±1.0	38±2.0	36.1±1.7
Ws-Ca	6.0±0.1	8.5±0.5	3.3±0.2	0.13±0.0	2.2±0.1	14.1±0.8	22±0.6	63±2.8	54.3±3.2
Es-An1	5.3±0.1	6.8±1.1	1.8±0.3	0.14±0.0	1.1±0.2	9.9±1.4	57±0.8	17±2.5	19.5±1.4
Es-An2	5.8±0.2	6.9±1.0	1.8±0.2	0.10±0.0	1.8±0.2	10.5±1.0	45±1.8	24±3.3	18.7±2.0
Es-Ni	5.5±0.2	6.5±1.0	1.8±0.2	0.14±0.0	1.8±0.2	10.2±1.1	30±1.2	34±3.6	34.4±2.8
Es-Fe	5.1±0.1	4.3±0.3	1.6±0.1	0.10±0.0	1.8±0.1	7.8±0.6	25±0.8	31±2.0	21.1±3.5
LSD[a]	0.6	3.0	0.8	0.03	0.7	3.7	4	10	9.7

Values are the mean ± SE (standard error) (n=10)

ECEC Effective cation exchange capacity (sum of exchangeable cations), *CEC* cation exchange capacity, *BS* base saturation (ECEC/CEC×100)

[a] Least significant difference (LSD) is given for each characteristic (α=0.01)

Table 3 Average contents of elements, and total reserve in Ca, Mg, Na, K (TRB) in the fine earth (<2 mm) of soil samples from the six experimental sites (ten plots per site)

Soil	Total element content/g kg^{-1}										TRB[a]/$cmol_c\ kg^{-1}$
	Si	Al	Fe	Ca	Mg	Na	K	Mn	P	Ti	
Ws-An	241±3.4	90±2.1	70±2.3	13.7±0.9	9.9±0.4	6.5±0.5	5.1±0.3	1.6±0.1	2.2±0.2	5.3±0.3	191±9.9
Ws-Ca	262±1.7	89±1.4	73±1.5	24.2±1.2	11.2±0.8	10.4±0.2	4.7±0.2	1.4±0.0	1.0±0.1	5.4±0.1	270±11.9
Es-An1	159±3.4	104±1.7	85±1.6	5.7±0.7	10.6±1.1	1.6±0.2	3.3±0.5	1.6±0.3	2.0±0.1	6.6±0.2	131±13.2
Es-An2	158±4.1	137±2.9	100±2.5	4.4±1.1	6.3±0.6	1.2±0.1	2.6±0.1	2.4±0.2	1.9±0.1	7.4±0.3	86±6.6
Es-Ni	193±4.1	135±3.1	104±1.7	3.9±0.6	4.4±0.5	1.5±0.3	3.0±0.2	3.1±0.2	1.6±0.1	8.8±0.4	70±8.5
Es-Fe	180±4.6	136±2.9	111±2.1	1.4±0.1	1.4±0.0	0.3±0.0	2.6±0.2	3.4±0.7	1.2±0.1	9.4±0.1	26±1.2
LSD[b] 14	14	9	7	3.2	2.5	1.0	1.1	1.3	0.5	0.9	36

Values are the mean ± SE (standard error) (n=10)

[a] TRB (total reserve in bases) is the sum ($cmol_c\ kg^{-1}$) of total contents of Ca, Mg, K, Na (Herbillon 1986)

[b] Least significant difference (LSD) is given for each element (α=0.01)

significantly smaller in the Es (2.73–3.91 g kg^{-1}) than in the Ws sites (7.66–9.64 g kg^{-1}). The significantly highest Si concentration was measured in the Cambisol Ws-Ca. Within the Eastern transect, the average leaf Si concentrations did not significantly differ between soils. The plant nutrient concentrations revealed adequate plant nutrition with respect to Ca, Mg, K, P and Mn (Table 4). The average leaf concentrations of Mn were significantly larger in Es-Ni and Es-Fe than in other soils, likely because of the large contents of Mn oxide in these strongly weathered soils (Ndayiragije 1996).

Figure 2 shows the Si concentration in each leaf as a function of leaf age from the sampling of one plant per representative plot per site. For each leaf age, Si concentration was larger for Ws soils than for Es soils. The Si concentration was strongly correlated to the leaf age in all soils (r=0.88, 0.93, 0.92, 0.81, and 0.96, for Es-An1, Es-An2, Es-Ni, Ws-An, and Ws-Ca, respectively), except in Es-Fe (r=0.08). Figure 2 also shows that the accumulation rate of Si in banana leaves was much larger in plants cropped on Ws soils than on Es soils.

Discussion

Soil weathering stage and chemical properties

The data presented in Table 3 show that the volcanic ash soils under study differ in weathering stage, in good agreement with previous studies (Colmet-Daage and Lagache 1965; Colmet-Daage and Gautheyrou 1974; Ndayiragije 1996; Ndayiragije and Delvaux 2003, 2004). These studies converge to show that weathering stage was directly related to the annual

Table 4 Average values of the Si and nutrient concentrations (g kg^{-1} DM) in banana leaf samples (external part of the lamina of leaf III) in the six experimental sites (ten plots per site)

Soil	Total elemental concentration/g kg^{-1} DM						
	Ca	Fe	K	Mg	Mn	P	Si
Ws-An	4.86±0.26	0.07±0.00	31.83±0.62	3.25±0.04	0.37±0.05	2.00±0.03	7.66±0.75
Ws-Ca	4.87±0.15	0.05±0.00	33.29±0.44	3.20±0.07	0.44±0.02	2.21±0.06	9.64±0.68
Es-An1	4.14±0.32	0.07±0.00	29.46±0.65	2.90±0.06	0.40±0.07	2.07±0.05	3.35±0.30
Es-An2	4.58±0.40	0.06±0.00	32.34±0.70	3.19±0.16	0.48±0.06	2.13±0.04	2.75±0.20
Es-Ni	5.49±0.23	0.05±0.00	29.02±0.51	3.07±0.07	1.30±0.24	1.83±0.04	3.91±0.42
Es-Fe	6.57±0.22	0.09±0.00	28.31±0.56	3.23±0.05	1.50±0.11	2.02±0.03	2.73±0.20
LSD[a]	1.04	0.01	2.22	0.33	0.44	0.16	1.82

Values are the mean ± SE (standard error) (n=10)

[a] Least significant difference (LSD) is given for each element (α=0.01)

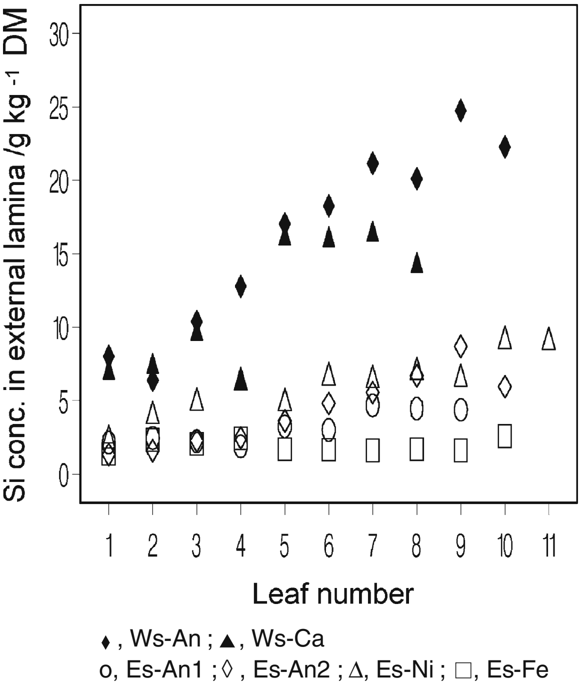

Fig. 2 Relationship between the leaf Si concentration in banana (external part of the lamina) and the leaf position related to the sequence of leaf emergence (each point of the graph corresponds to one leaf sample)

precipitation and age of parent material. Since weathering depletes primary minerals, elements are lost to leaching. Figure 3 shows that the loss of Si and TRB (Ca, Mg, K, Na) parallels a relative concentration of Al and Fe, confirming previous data obtained in various tropical volcanic environments (Delvaux et al. 1989; Nieuwenhuyse et al. 1994; Chadwick et al. 2003; Delfosse et al. 2005). In our soils developed on similar andesitic ash, the concomitant decrease of the total Si content and TRB (r=0.74) reveals the advanced weathering stage of the Es soils relatively to Ws (Table 3, Fig. 3). The loss of Si and base cations (TRB) results in a relative accumulation of Al and Fe (r=−0.87 and r=−0.86, respectively). It also induces a relative accumulation of titanium (Fig. 4), a poorly mobile element in soils: Ti content is negatively correlated with Si content (r=−0.55) and TRB (r=−0.83). Table 3, Figs. 3 and 4 all illustrate that Es-soils are more weathered than Ws-soils. The lowest TRB values (21–32 $cmol_c\ kg^{-1}$) measured in Es-Fe are typical for strongly weathered ferrallitic soils (Herbillon 1986). Rainfall and the amount of water available to leach elements from soil are major features determining weathering, soil constitution and exchange properties (Chadwick et al. 2003). Figure 5a illustrates the negative impact of the amount of annual precipitation on Si content of soils (r=−0.69). Yet, Ws-An and Ws-Ca do not follow the general trend observed for Es-soils, as they exhibit larger soil Si contents than Es-soils at given MAR value. These features are caused by less advanced weathering (see TRB in Table 3; Fig. 4) and the nature of dominant secondary clay minerals denoting the presence of smectite in Ws-Ca (Table 1), the stability of which is linked to relatively high concentration of aqueous H_4SiO_4 (Karathanasis 2002). In Es-soils, intense weathering and leaching led to stronger mineral depletion and desilication (Table 3, Figs. 4 and 5), and to the synthesis of secondary oxides and 1:1 clay minerals typical for such conditions (Table 1). Noteworthy is the fact that gibbsite is a dominant secondary constituent in the Es-Andosols (Table 1; Ndayiragije and Delvaux 2003). The linear decline of base saturation with respect to MAR (r=−0.74; Fig. 5b) further illustrates the depletion of exchangeable cations in strong leaching conditions, despite of regular fertilization as practiced in intensive banana cropping systems.

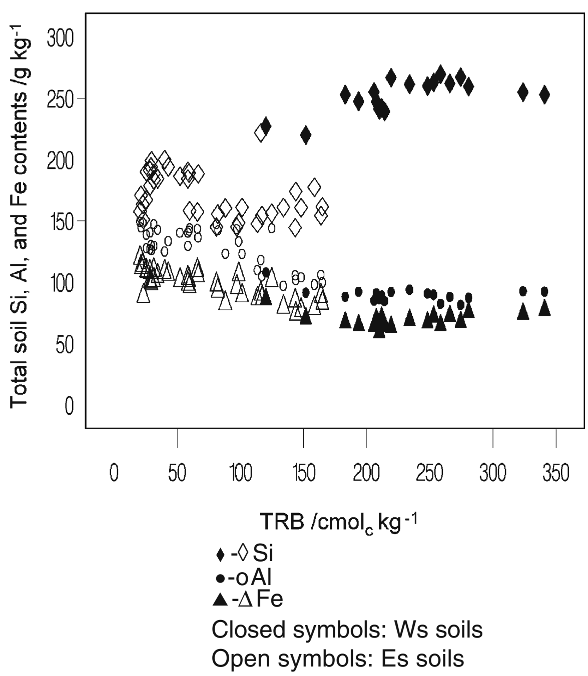

Fig. 3 Relationship between total Si, Al, Fe contents and total reserve in bases (*TRB*) in the 60 soil samples from the six experimental sites. *Ws* Western slopes, *Es* Eastern slopes

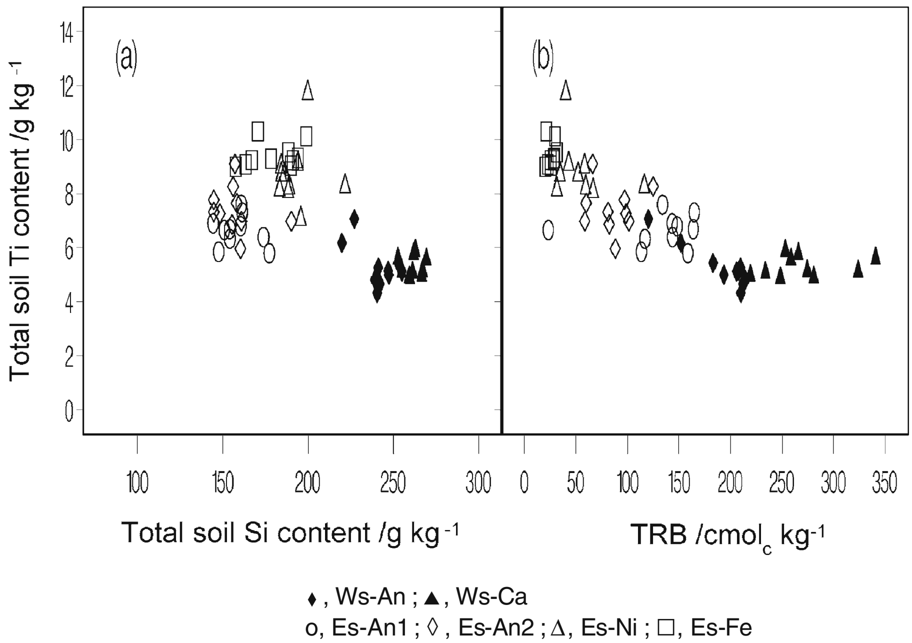

Fig. 4 Relationship between soil Ti content and: **a** total Si content, **b** total reserve in bases (TRB) in the 60 soil samples from the six experimental sites. *Ws* Western slopes, *Es* Eastern slopes

Leaf silicon concentration of banana plant reveals the weathering stage of soils

To the best of our knowledge, we report here the first values of leaf concentrations of silicon in mature banana plants, purposely sampled at flowering stage for foliar diagnosis using international standards (Martin-Prével 1980). The banana plant is a silicon-accumulator (Henriet et al. 2006). The average leaf Si concentrations (Table 4: 2.73–9.64 g kg^{-1}) are within the range of leaf Si concentrations measured in young banana plantlets (0–14 g kg^{-1}) cultivated in hydroponics (Henriet et al. 2006). The average leaf Si concentrations in mature banana plants are below the leaf Si concentrations of other Si-accumulators such as rice (*Oryza sativa*) (63 g kg^{-1} DM) and wheat (*Triticum aestivum* L.) (14.4 g kg^{-1} DM) (Ma and Takahashi 2002, and references therein). They are, however, similar to those measured in sugarcane (*Saccharum officinarum* L.) (7.7 g kg^{-1} DM), another well-known Si accumulator (Ma and Takahashi 2002).

The leaf Si concentration in banana is strongly correlated with soil $CaCl_2$-extractable Si content (r=0.85), total Si content (r=0.85), and TRB (r=0.82) (Fig. 6). The $CaCl_2$-extractable Si content is directly related to the concentration of Si in soil solution, and thus provides a convenient test to predict the availability of soil Si for plants, as shown for different plant species cropped in other soil types (Haysom and Chapman 1975; Chapman et al. 1981; Berthelsen et al. 2001). Figure 6a supports this assessment. In hydroponics, Si status of young banana plantlets is controlled by the concentration of Si in the nutrient solution (Henriet et al. 2006). The present data corroborate this conclusion for mature banana plants sampled in cultivated plots, since the $CaCl_2$ extractant is recognised to provide a measure of readily available Si (Chapman et al. 1981). Figure 6 further shows that the bioavailability of silicon, as measured by the leaf Si concentration of mature banana plants, strongly differs between Ws and Es-soils, and is directly related to silicate reserve and soil weathering stage. The leaf Si concentration as well as the $CaCl_2$-extractable Si content, soil Si content and TRB all decrease in the sequence Ws-Ca > Ws-An > Es-Ni > Es-Fe = Es-An2 = Es-An1. The bioavailability of silicon is the lowest in the Es gibbsitic perhydrated Andosols and in the Ferralsols, where it is linked to Si depletion (Fig. 6), and to the relative accumulation of secondary oxides and Si-poor aluminosilicates (Fig. 3, Table 1). Our experimental data thus suggest that Si concentration in the soil solution may control the uptake of silicon by banana plants and thus impact the leaf Si concentration. In turn, the concentration of aqueous Si in soil is controlled by soil mineral constitution (Kittrick 1969; Karathanasis 2002). The dissolution of weatherable minerals is probably a major

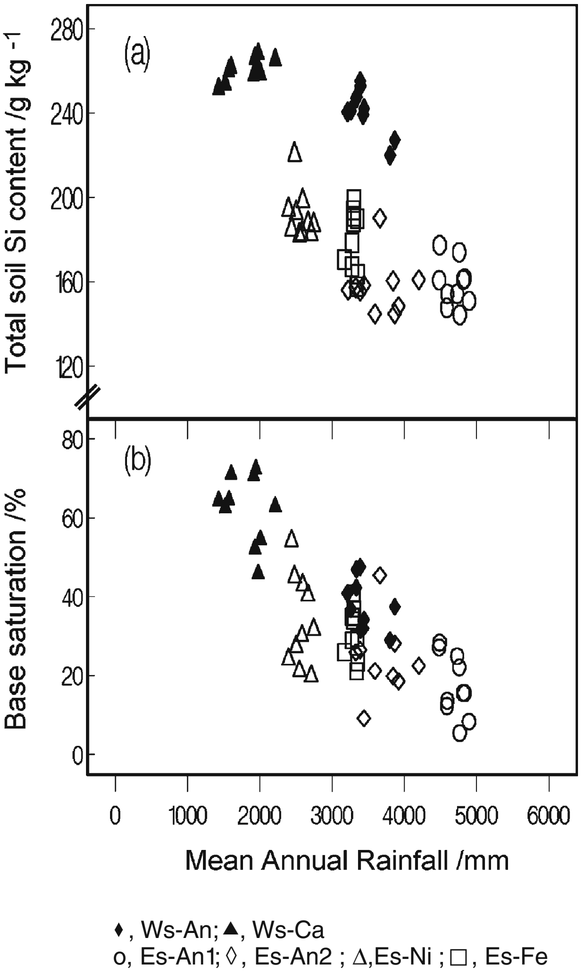

Fig. 5 Relationship between **a** total Si content and **b** base saturation in the 60 soil samples from the six experimental sites and mean annual rainfall, as computed according to Chaperon et al. (1985) for each plot

process promoting the soil-to-plant transfer of silicon. Bananas are very high nutrient-demanding plants characterized by exceptional requirements of potassium (Lahav 1995). The excess of cation over anion uptake promotes a large excretion of protons by banana roots (Rufyikiri et al. 2001), and thereby a dissolution of weatherable minerals (Hinsinger et al. 2001; Rufyikiri et al. 2004). In our case study, the silicon content of mature banana leaves is therefore linked to soil constitution and weathering stage, in turn depending on MAR and age of parent material, as discussed above.

The large proportions of Ca and Mg in the TRB of the least weathered soils (Table 3) are linked to the composition of the parent ash, dominated by plagioclase, pyroxene and ferromagnesian glass (Dagain et al. 1981; Ndayiragije 1996). The strong and positive correlation between the leaf Si concentration and the content of non-exchangeable Ca and Na in soils (r= 0.88; Fig. 7a) suggests that Ca and Na volcanic glasses and possibly plagioclase (Hinsinger et al. 2001) may contribute to the pool of plant-available Si. The weaker correlation between the leaf content of Si and the content of non-exchangeable Mg (r=0.56; Fig. 7b) suggests that part of silicate Mg may not readily contribute to that pool. Contents of non-exchangeable Mg above 50 $cmol_c\ kg^{-1}$ are related to Si leaf concentrations generally above 6 $g\ kg^{-1}$ in Ws soils, but below 4.5 $g\ kg^{-1}$ in the Es Andosols Es-An1 and Es-An2. The relatively low contribution of Mg bearing silicates to the pool of plant-available Si in the Es Andosols may be due to the combination of two factors: the coating of weathered particles of ferro-magnesian minerals by secondary minerals, as shown by micromorphological investigations (Ndayiragije 1996), and the occurrence of hydroxy-Al-interlayered 2:1 clay minerals (Table 1). Oxide and clay coatings can stabilize weathered primary minerals and protect them from further dissolution (Baert and Van Ranst 1997; Certini et al. 2006). The hydroxy-Al-interlayered 2:1 clay minerals contain Mg in their octahedral sheet (Ndayiragije 1996; Ndayiragije and Delvaux 2003). Al-interlayering protects these minerals from weathering (Brahy et al. 2000), as they are as stable as kaolinite in soil environments (Karathanasis et al. 1983; Karathanasis 1988). These statements further support that the pool of plant-available Si would be replenished by readily weatherable minerals in current soil conditions.

As illustrated in Fig. 2, banana leaves accumulate silicon continuously throughout their life cycle. Our data also illustrate the larger relative accumulation of Si in older leaves vs younger leaves in the Ws environments. Excluding data from Es-Fe, we computed Ws- and Es-regression lines. The regression slopes (Ws: 1.92; Es: 0.62) are significantly different (p<0.0001). The steep gradient of Si leaf concentration in the Ws soils can be explained by their larger Si bioavailability and possibly by the water balance.

The water balance (rainfall minus potential evapotranspiration) may indeed have affected the transfer of Si from soil to the banana plant, since silicon deposition in plants depends also on their transpiration rate (Jones and Handreck 1967). However, the

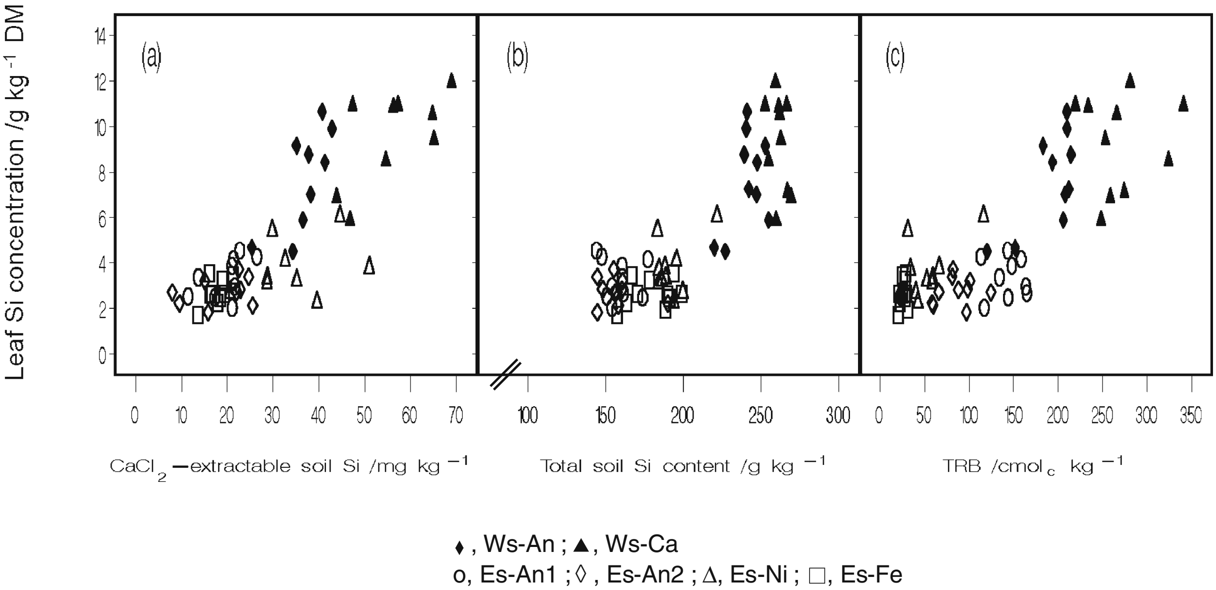

Fig. 6 Relationship between the leaf Si concentration in banana (leaf III, external part of the lamina) and: **a** the soil $CaCl_2$-extractable Si content, **b** the total content of Si in soil, **c** TRB in the 60 soil samples from the six experimental sites. *Ws* Western slopes, *Es* Eastern slopes

banana plants were sampled after the long rainy season extending from April to January, i.e. a period of precipitation surplus over potential evapotranspiration. Besides, within the wettest areas (MAR > 3,000 mm; Table 1), the largest leaf Si concentrations actually occurred in banana plants cropped on the least weathered soils Ws-An. A complementary study carried out in controlled conditions of water balance supports that soil weathering stage directly governed the soil-to-plant transfer of silicon (Henriet et al. 2008).

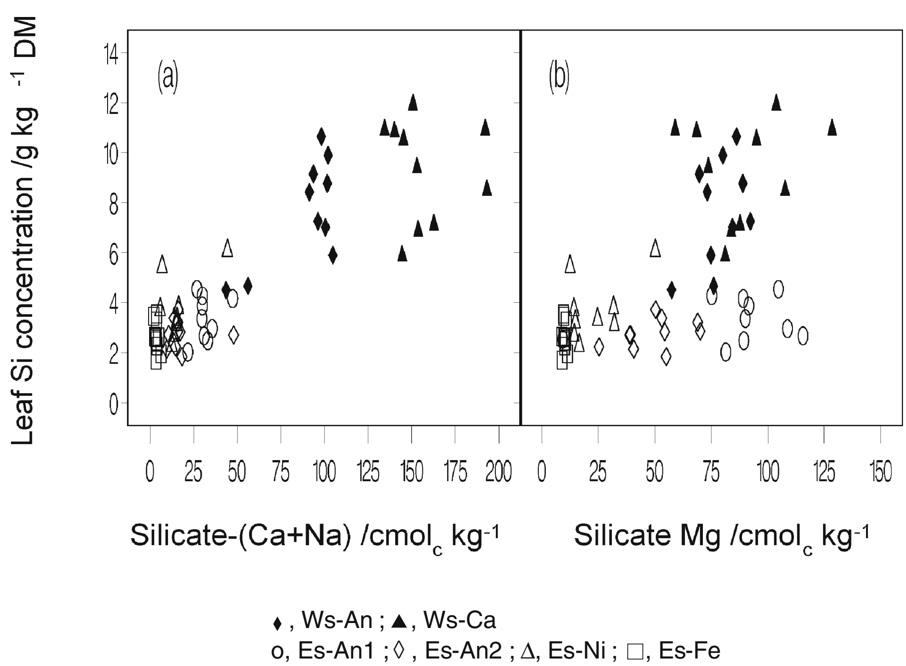

Fig. 7 Relationship between the leaf content of Si in banana (leaf III, external lamina) and: **a** silicate-(Ca+Na), and **b** silicate-Mg (silicate-element content = total element content minus exchangeable element content) in the 60 soil samples from the six experimental sites. *Ws* Western slopes, *Es* Eastern slopes

Conclusion

The leaf concentration of silicon in mature banana plants cropped on volcanic soils developed from andesitic ash ranged from 1.7 to 12 g kg^{-1} depending on the availability of Si in soil, as measured through $CaCl_2$-extraction. Silicon availability was governed by soil constitution, and thus weathering stage: the lowest leaf Si concentrations were measured for banana plants cropped on strongly desilicated soils such as gibbstic Andosols and Ferralsols. Conversely, the highest leaf Si concentrations corresponded to the least weathered soils.

We conclude that the Si content of banana leaves reveals the weathering stage of soils developed from similar volcanic ash. Supporting previous assessments (Chadwick et al. 2003), we further conclude that such volcanic environments provide remarkable natural laboratories to conduct weathering and pedology research, as well as soil-to-plant transfer studies.

Acknowledgements We are grateful to N. De Jaeger, K. Henin, A. Iserentant and C. Givron for their strong analytical and technical support. C.H. is supported by the "Fonds pour la formation à la Recherche dans l'Industrie et dans l'Agriculture" (FRIA) of Belgium, and X.D. is a Research Associate of the "Fonds National de la Recherche Scientifique" (FNRS) of Belgium.

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