



Is silicon beneficial for cassava (*Manihot esculenta* Crantz)?

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Abstract

Background and aim Ranked among the world's top ten crops, cassava (*Manihot esculenta* Crantz) is the main staple food in sub-Saharan Africa. Its production is strongly limited by biotic and abiotic stresses, which proved to be mitigated in other plants by silicon (Si) uptake. The role of Si is unknown in cassava. Yet it has genes encoding specific aquaporins involved in plant water and Si influxes in numbers similar to those of some Si accumulating monocots.

Methods Cassava Si and nutrient status were studied in four sites in South-Kivu, Democratic Republic of Congo, differing in altitude, climate and soil desilication stage. Out of 720 farms, 360 plots were

selected for agronomic monitoring, of which 40 for foliar/topsoil analysis using germanium to trace Si.

Results Regardless of soil type, Si concentration in cassava leaves ranged from 2 to 14 g kg⁻¹ while root yield varied from 0.5 to 18 t ha⁻¹ yr⁻¹. Silicon accumulation formed fine-sized phytoliths of different morphotypes. Structural equation modelling showed that leaf Si mineralomass was an important predictor of yield, with a direct contribution of 45%. Silicon accumulation mitigated the altitude-mediated incidence of cassava mosaic disease (25%), notably through enhancing micronutrient uptake, while it could contribute to the plant tolerance to soil acidity.

Conclusion Silicon accumulates substantially in cassava leaves. Our data highlight the potential role of Si in cassava production through direct and indirect effects by alleviating biotic and abiotic stresses. The function of Si in cassava thus deserves more attention than given until now.

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Introduction

Cassava (*Manihot esculenta* Crantz) ranks in the 10 most economically important crops on Earth in terms of global production (<https://ourworldindata.org>). It is a major food crop in Africa and a source of calories for millions of Africans (Achidi et al. 2005; Munyahali et al. 2017) due to the high starch content ($\geq 90\%$ of dry matter) of its tuberous roots (Moorthy and Padmaja 2002). In the Democratic Republic of Congo (DRC), cassava is the main staple food for the population and its production generates income for many farmers (Lema et al. 2004; Munyahali et al. 2017). Because of its tolerance to various stresses, cassava is generally grown on poor soils, with little or no human-applied inputs, e.g., fertilizers, pesticides, irrigation water (Howeler 2002), hence yields have stagnated at a low national level of $\sim 8 \text{ t ha}^{-1} \text{ yr}^{-1}$ for decades (<https://ourworldindata.org>). Soil infertility is a common trait of most cassava growing areas (Howeler 2002), particularly in DRC (Pypers et al. 2011). As cassava is responsive to fertilizers (Howeler 2002; Fermont et al. 2010), integrated soil fertility management (Vanlauwe et al. 2010) increases root yield and net income (Pypers et al. 2011). In South-Kivu, DRC, cassava is generally grown continuously on small plots due to high population density and land scarcity (Munyahali et al. 2017). Mineral deficiencies, water stress and plant diseases are common constraints in this region (Ouma et al. 2011). Cassava mosaic disease (CMD) is one of the most severe obstacles to crop production (Bisimwa et al. 2019; Obonyo et al. 2007; Shukuru et al. 2022), while cassava brown streak disease (CBSD), also caused by viruses, is a rising threat (Kwibuka et al. 2022). Climate change observed since 1992 has led to variations in cassava yields of 17 to 40% due to delayed and/or reduced rainfall, which has aggravated pest damage and required a reorganization of the agricultural calendar (Cirimwani et al. 2019).

Silicon (Si), although not essential, has a number of beneficial effects on a variety of plant species, acting as an extracellular prophylactic agent against biotic and abiotic stresses including pests, diseases and water stress (Coskun et al. 2019). These beneficial effects were particularly highlighted in monocots, but less frequently reported in dicots (Rodrigues et al. 2015; Kovács et al. 2022). Silicon status and role in cassava are virtually unknown. Once absorbed as

monosilicic acid (H_4SiO_4), Si is translocated to plant shoots where it precipitates as amorphous, hydrated silica ($\text{SiO}_2 \cdot n\text{H}_2\text{O}$) forming relatively stable phytoliths (Jones and Handreck 1965) or fragile siliceous structures (Puppe et al. 2017). Phytogenic silica bodies in cassava were scarcely reported (Adebisi et al. 2019; Ezell et al. 2006; Watling et al. 2018). While silicified hair cells were recognized early in cassava (Piperno 1981), phytoliths long remained unidentified in this plant (Carey and Fulweiler 2016; Piperno 1991). Detectable silica bodies were reported in the tuber periderm (Adebisi et al. 2019) while cassava phytoliths were tentatively described in leaf tissues (Ezell et al. 2006) and sediments (Watling et al. 2018). Njenga et al. (2017) provided the first evidence of the potential role of Si in inducing resistance in cassava to bacterial blight under controlled conditions. On the other hand, the ability of some cassava varieties to tolerate water stress and regulate water efflux is due to specific aquaporins (AQPs) controlling stomatal closure (Putpeerawit et al. 2017; Yu et al. 2016), hence promoting drought resilience of cassava (Pushpalatha and Gangadharan 2020). Certain AQPs, named Lsi (Ma et al. 2006; Saitoh and Suga 2022), are Nodulin 26-like intrinsic proteins (NIPs) involved in the cellular influx of Si and its movement in the plant (Coskun et al. 2019). The phylogenetic distribution of these Si influx transporters in plants includes monocots and dicots (Coskun et al. 2019). Interestingly, their number in cassava genome (Putpeerawit et al. 2017) is similar to that in maize and rice (Deshmukh and Bélanger 2016), well-known Si accumulators.

Here we take advantage of a regional study aimed at identifying and prioritizing factors limiting cassava yield in 720 small farms to focus on the Si status in soil-cassava systems in South-Kivu. We analyze topsoils and cassava leaves in 40 cultivated plots. We determine germanium (Ge) concentrations in topsoils, leaves and phytoliths using the Ge/Si ratio as a proxy to decipher the soil-to-plant transfer of Si (Wiche et al. 2018). Our objective is threefold: (i) to evaluate the range of leaf Si concentrations in cassava grown on soils differing in desilication stage, detect the source of plant available Si in soil, and quantify Si uptake by cassava, (ii) to infer the impact of plant Si status on root yield and viral disease incidence in smallholders' plots farmed with very low to no inputs, (iii) to isolate and analyze cassava phytoliths.

Materials and methods

Environmental framework

The environmental context of South-Kivu is marked by significant geological, soil and climatic diversity (Ngongo et al. 2009). The study area comprises three territories of the province: Walungu, Kalehe and Uvira with respective areas of 800, 5707 and 3146 km². Köppen climates Aw and Cw are recognized (Beck et al. 2018). Four sites were selected: Mushinga (Walungu), Bunyakiri (Kalehe), Runingu and Kiliba (Uvira), abbreviated as Mu, Bu, Ru and Ki, respectively. The sites differed in altitude (780–1980 m asl) and climate (Table 1). Highest sites Mu and Bu were wetter and cooler than Ru and Ki. Mu and Bu soils derived from ancient basalt and basement rock, respectively, and key out as Ferralsol and Acrisol (IUSS 2015) in which kaolinite is the predominant clay mineral. They have undergone prolonged desilication due to advanced weathering with TRB below the upper limit (40 cmol₍₊₎ kg⁻¹) of the ferrallitic domain (Herbillon 1986) and low Si_t/(Al_t+Fe_t) ratio, particularly in the strongly desilicated Mu soil containing gibbsite (Table 1). In contrast, Ru and Ki soils (Cambisol, Fluvisol), developed from holocene lacustrine deposits, were moderately weathered with

TRB around 200 cmol₍₊₎ kg⁻¹ and relatively high Si_t/(Al_t+Fe_t) ratio, indicating much less desilication. Topsoil samples were analyzed for basic physico-chemical properties (Table S1). Highest organic carbon (OC) contents were found in Mu and Bu topsoils, at the highest altitudes. Topsoils were clearly sandier in Uvira (Ki, Ru) and more clayey in the most weathered soils (Mu, Bu) with much lower levels of available phosphorus (P) and pH. Only Bu topsoils may have acidity-related constraints.

Five-level experimental design

The sampling strategy is illustrated in Fig. 1. In the three territories (Table 1), we chose villages with high cassava production based on the availability of cultivated fields, accessibility and security. The sampling frame was multi-level, with the farm household as sampling unit. (1) Working with each village chief, we identified 720 smallholders (240/territory) to conduct a socio-economic survey, which is presently analyzed elsewhere. (2) Within these 720 farms, 360 plots (120/territory) with 3-month-old cassava fields were selected randomly for agronomic monitoring, the data from which are presently analyzed elsewhere. Randomness was achieved using an arithmetic progression

Table 1 Altitude, climate, geology and soil characteristics in the four studied sites in South Kivu, DR Congo

Territory	Site (altitude, m asl)	Coordinates	MAR ¹ Mm	MAT ² °C	Soil parent rock	Soil type ³	Soil weathering index in A and B horizons	
							TRB ⁴ cmol ₍₊₎ kg ⁻¹	Si _t /(Al _t +Fe _t) ⁵ mol mol ⁻¹
Walungu	Mushinga – Mu (1570–1980)	02°75'S 28°68'E	1620	18.4	Cenozoïc, Miocene tholeiitic basalt	Ferralsol	A: 27	0.98
							B: 28	0.85
Kalehe	Bunyakiri – Bu (1000–1220)	02°09'S 28°59'E	1637	21.1	Precambrian, Mesoproterozoïc granito-gneiss	Acrisol	A: 27	2.42
							B: 19	1.49
Uvira	Runingu – Ru (780–920)	03°20'S 29°15'E	986	25.0	Holocene lacustrine sediments	Cambisol	A: 180	4.92
						Fluvisol	B: 196	3.68
	Kiliba – Ki (780–930)	03°25'S 29°18'E	980	25.1	Holocene lacustrine sediments	Cambisol	A: 210	4.01
						Fluvisol	B: 219	3.64

¹ Mean Annual Rainfall

² Mean Annual Temperature

³ WRB Reference Soil Groups (IUSS 2015)

⁴ Total Reserve in Bases: sum of elemental contents (Herbillon 1986)

⁵ Molar ratio of total elemental content of Si vs the sum of total elemental contents of aluminum (Al) and iron (Fe)

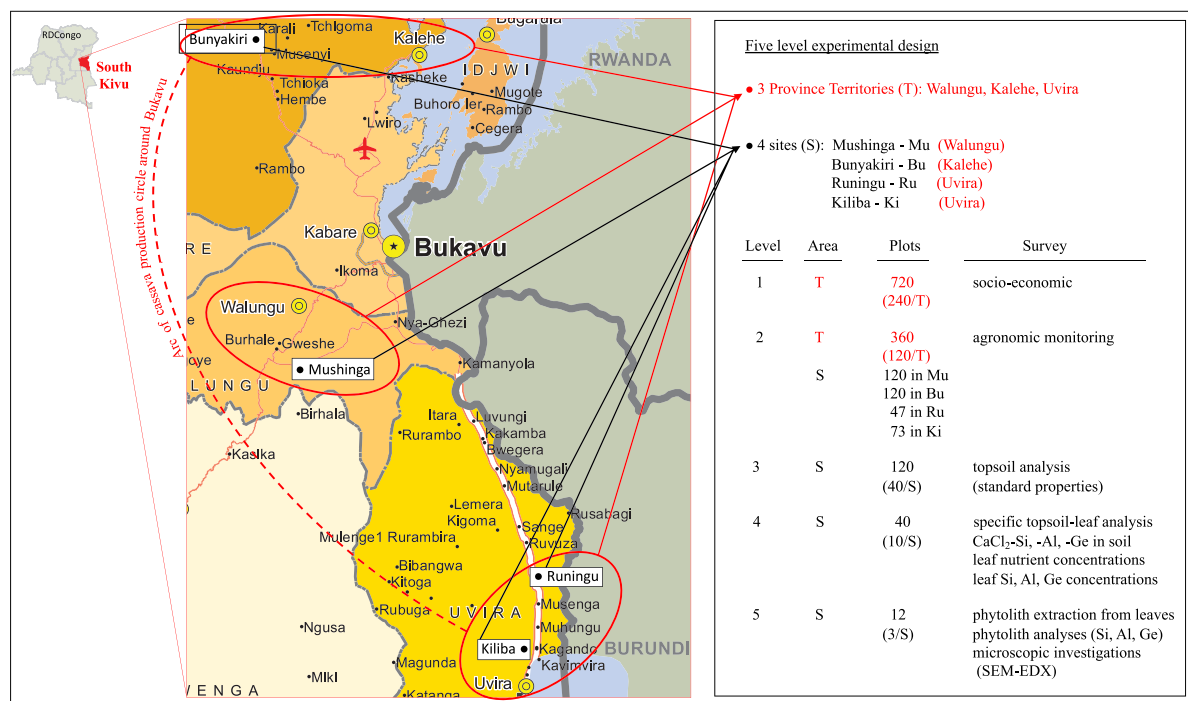


Fig. 1 General scheme illustrating the sampling strategy with decreasing number of cultivated plots from level 1 to 5. At each given level, the plots were systematically selected from the plot's population of the previous level, by randomization from level 1 to 2 and 2 to 3, by sorting on the basis of root

yield from level 3 to 4, and of the Si leaf concentration from level 4 to 5. Cartographic data were obtained from a free, open, collaborative platform (Common geographical reference of DRC; <https://www.rgc.cd>)

starting from plot N°2 (2/4/6/...) or N°3 in case of inadequate planting time or safety (3/6/9...). The 360 plots were distributed across the sites as follows: 120 (Mu), 120 (Bu), 47 (Ru) and 73 (Ki). In each plot, 3 quadrats were delimited, each being a 5 m x 5 m square study area of 25 m². Monitoring was carried out in each quadrat. It focused on cassava physiological parameters, weed cover, disease incidence, management practices, measurement of leaf biomass and root yield at harvest. (3) Soil characterization was carried out in 120 of the 360 plots (40/site), selected randomly. (4) Forty plots (10/site) reflecting the range of cassava root yields were selected for specific soil and leaf analyses. (5) From these, 12 leaf samples (3/site) were selected based on leaf Si concentrations, Si/Al and Ge/Si ratios, in order to detect and analyze cassava phytoliths. As a matter of fact, our present study involves levels 4 (40 plots) and 5 (12 plots). However, it considers field data obtained from level 2 for CMD incidence, leaf biomass, root yield, and the use of

local or improved variety, as registered in the 40 plots of level 4, out of the 360 plots of level 2.

Topsoil sampling and analyses (level 4 of experimental design)

Topsoil subsamples were collected with an auger at 0-25 cm (plough layer). In each quadrat, two diagonals were drawn to take 1 subsample at the intersection and 4 halfway between the edge and the intersection, the mixed 5 subsamples forming 1 composite sample per quadrat. The 40 samples were air-dried, sieved at 2 mm, and analyzed for their standard properties (Table S1). The respective concentrations of bioavailable Si (CaCl₂-Si) and amorphous Si (ASi) in topsoils were determined by (i) 0.01 M CaCl₂ extraction (Haysom and Chapman 1975; Sauer et al. 2006) and (ii) 0.1 M Na₂CO₃ dissolution (pH 11.2) (DeMaster 1981; Koning et al. 2002; Sauer et al. 2006), both in triplicates. (i) For each sample, 2 g: 20 ml soil:CaCl₂ suspension

was shaken for 16 h, and centrifuged ($3400 \times g$, 10 min). The supernatant (15 ml) was filtered and separated into 2 aliquots to measure $\text{pH}_{\text{CaCl}_2}$ (5 ml) and solute concentrations (10 ml). The latter extract was separated into 2 aliquots of 5 ml to determine Si and aluminum (Al) concentration by Inductively Coupled Plasma—Atomic Emission Spectrometry (ICP-AES, Jarrell Ash Iris Advantage) and Ge concentration by ICP Mass Spectrometry (ICP-MS), respectively. Each 5 ml aliquot was diluted with Milli-Q water by 10 times before dosing Si and Al, but by 2.5 times for Ge. In both cases, each 5 ml aliquot was acidified by adding 50 μl 7 M HNO_3 . The CaCl_2 extractable Si, Al and Ge concentrations were used to calculate the values of the Al/Si and Ge/Si atomic ratio. (ii) From the 40 samples, 12 were selected based on their properties (Table S1) and CaCl_2 -extractable Si contents for the extraction with 0.1 M Na_2CO_3 . Each 30 mg: 40 ml soil: Na_2CO_3 suspension was digested for 5 h at 85 °C. One milliliter of extraction solution was collected at 2, 3, 4 and 5 h, then neutralized and acidified by adding 100 μl of 7 M HNO_3 to analyze dissolved Si and Al using ICP-AES. The kinetic evolution of extracted Si and Al were used to estimate the contents of ASi and amorphous Al (AAI) as described in Li et al. (2022).

Foliar sampling and analysis (level 4)

Cassava leaves were taken from 4 plants located at each edge of a 1 m² square in the middle of the quadrat. Well-developed leaves of different ages were collected from the green canopy (Munyahali et al. 2017) and assembled to form a composite sample per study area. They were carefully washed to remove any dust, air-dried and oven-dried at 60 °C for 4 days. Mineral analysis was carried out after calcination at 450 °C for 1 day and fusion in Li-metaborate + Li-tetraborate at 1000 °C (Chao and Sanzalone 1992), followed by ash dissolution with concentrated HNO_3 . Plant nutrients (C, N, K, Ca, Mg, P, S, Fe, Mn, Zn, Ni, Cu), Si, Al and Ge concentrations were measured by ICP-AES and ICP-MS, respectively, allowing to calculate the values of the leaf Al/Si and Ge/Si ratio. Of the 40 foliar samples, 12 were selected based on Si and Ge concentrations for phytolith detection.

Detection and analyses of phytoliths (level 5)

Dry ashing followed by wet digestion has proved not to affect phytolith morphological properties (Parr et al. 2001a, b). Five grams of leaf material (3 replicates) was rinsed with deionized water, 1 M HCl and 70% ethanol (Kelly 1990), oven-dried at 45 °C for 48 h, grinded and calcined at 450 °C for 8 h. The ash was treated with 15 ml of 10% HCl, then in a mixture of $\text{HNO}_3/\text{H}_2\text{O}_2$ (70/30%) in a water bath at 70 °C for one week until complete mineralization of OC. Phytolith particles were washed using a deionized water cycle by washing-centrifugation-filtration (13,100 rpm, 5 min) until constant pH and electrical conductivity equal to that of the deionized water (Li et al. 2023). Phytoliths were then oven-dried at 45 °C for 48 h, weighed and separated in 3 aliquots for further analyses: (i) Scanning Electron Microscopy (SEM), (ii) determination of Si, Al and Ge concentrations. (i) SEM images were performed using a field emission gun SEM (FEG-SEM; Zeiss Ultra55), equipped with an EDX system (Jeol JSM2300 with a resolution < 129 eV) to assess the micro-scale distribution of elements: carbon (C), oxygen (O), iron (Fe), Al, and Si. (ii) Phytolith Si and Al concentrations were measured by ICP-AES following the procedure described above for foliar analysis, while Ge concentration was dosed by ICP-MS in powder samples (100 mg) after alkaline fusion using sodium peroxide (Na_2O_2) (Li et al. 2023). The Si, Al and Ge concentrations of extracted phytoliths were used to calculate the values of the Al/Si and Ge/Si atomic ratio.

Cassava variety type, CMD incidence, leaf biomass and root yield (level 2)

Agronomic monitoring reported only two types of cassava varieties, as designated by farmers: local and improved. Each type does not refer to a given germplasm, but to a set of cultivars. The local varieties are the ones used for years by several farmers' generations. The improved varieties are delivered by research centers and extension services as well as NGOs and international organizations. In South-Kivu, the improved varieties were introduced for various reasons: disease tolerance or resistance, crop performance, taste, precocity, flour quality, root dry matter and processing convenience.

Apart from CMD, CBSD also occurs in eastern DRC (Kwibuka et al. 2022). Symptoms due to these two viral infections can be distinguished by examination of leaves and stems 3 and 7 months after planting (MAP) and tubers (7 MAP) (Hillocks and Thresh 2000). This differential symptomatology was used in the field, but CBSD cases were very rare. The CMD incidence (I_{CMD}) was defined as the proportion of diseased plants (Bock et al. 2022; Moise et al. 2022):

$$I_{\text{CMD}} = [(\text{number of infected plants})/(\text{total number of plants})] \times 100$$

In each plot, I_{CMD} was measured at 3 and 7 MAP. All cassava plants were observed in three quadrats per plot. The number of plants per quadrat varied between sites with following ranges: 55–121 (Mu), 37–67 (Bu) 20–41 (Ru), 24–37 (Ki), reflecting the high planting density in Mu. Isolated cases of CBSD (Ru, Ki), absent at altitude (Mu, Bu), were not taken into account in determining I_{CMD} . Since whitefly (*Bemisia tabaci*) is the vector of CMD and CBSD, its presence in South-Kivu (Bisimwa et al. 2019; Macfadyen et al. 2018) was also noted in the quadrats. However, the ratings recorded were unreliable due to differences in the timeslot of observation, which had a considerable impact on the survey. Leaf biomass and root yield were measured at harvest (12 MAP) in the 360 plots. Cassava roots were collected from all cassava plants in each quadrat (3/plot) and their fresh weight was measured in the field. The total fresh leaf biomass of 4 plants was taken at each edge of a 1 m² square (1 m x 1 m) located in the middle of each quadrat (3/plot). Leaf samples were air-dried, and then oven-dried at 60 °C for 4 days to determine the dry leaf biomass.

Data treatment

To understand how plant Si affects crop yield and disease incidence (Cooke and Leishman 2011; Ma and Yamaji 2006), a structural equation model (SEMod) was used to disentangle the direct and indirect role of different drivers of crop yield and disease tolerance in the 40 plots corresponding to level 4 of the experimental design. Since SEMod separates the pathways of influence within a complex system, it can decipher network relationships that are typical in farming systems (Radujković et al. 2021; Ren et al. 2023). Variables

were pre-analyzed for skewed distributions to improve normality and linearity. Analyses were performed in R -version 4.3.2. Structural equation models were constructed using the *lavaan* package (Rosseel 2012), considering the influence of different variables in three steps. First, we tested the direct influence of altitude and uptake of Si, macronutrients and micronutrients (Fe, Mn, Zn, Cu) as key drivers for disease incidence and crop yield. Mineral uptake, or mineralomass, was cal-

culated as the product of nutrient concentration and leaf biomass. The sum of the four micronutrient uptakes was proposed to figure out the mineralomass of Fe, Mn, Zn and Cu instead of a composite (Radujković et al. 2021) or single uptakes (Wendling et al. 2016). Second, we investigated the indirect influence of Si uptake on crop yield through the impact of plant Si on disease tolerance (Coskun et al. 2019; Fauteux et al. 2005; Shittu et al. 2008). Third, we tested the indirect impact of Si accumulation in cassava on root yield through the interactions between Si and nutrients (Cooke and Leishman 2011; Coskun et al. 2019; Moise et al. 2019). The fit was assessed using standard indices: model chi-square (χ^2) $P > 0.05$, comparative fit index (CFI) > 0.95 , Tucker-Lewis index (TLI) > 0.95 , root mean squared error of approximation (RMSEA) < 0.08 , and standardized root mean square residual (SRMR) < 0.08 were considered as indicators of significant fit (Hooper et al. 2008; Schermelleh-Engel et al. 2003). In each step, we corrected goodness-of-fit index (GFI) for the model evaluation, significant (direct, indirect) paths and the highest R^2 was selected and reported. We further constructed a multiple regression model using the variables with a significant direct path on biomass in the final SEMod and partitioned the variance explained by nutrient uptake and disease factors. Model performance was evaluated via repeated (100 times) k-fold ($k = 10$) cross-validation using the caret package.

Results

CaCl₂ and Na₂CO₃ extractions from topsoils

Experimental data for CaCl₂ and Na₂CO₃ extractions are given in Tables S2, S3 and S4. The concentrations

of ASi and $\text{CaCl}_2\text{-Si}$ ranged from 0.3 to 3 g kg^{-1} for ASi, and from 13 to 130 mg kg^{-1} for $\text{CaCl}_2\text{-Si}$ (Fig. 2). Both were lowest in Bu and highest in Ru topsoils. The $\text{CaCl}_2\text{-Si}$ concentration increased with increasing $\text{pH}_{\text{CaCl}_2}$ (Fig. 3a) while $\text{CaCl}_2\text{-Al}$ concentration strongly decreased (Fig. 3b). The concentrations of $\text{CaCl}_2\text{-Al}$ and -Ge in Bu topsoils were significantly higher than those measured in Ru and Ki topsoils (Table S2). The acid Bu topsoils clearly stood out with higher Al/Si and Ge/Si ratios as well as lower $\text{pH}_{\text{CaCl}_2}$ values, ranging from 3.9 to 4.6 (Fig. 3c-d).

Mineral elements in cassava leaves

Mineral element concentrations are reported for selected plant nutrients (C, N, K, Ca, Mg, P, S, Fe, Mn, Zn, Ni, Cu) in Table S5 (detail) and Table 2 (summary), for Si, Al and Ge in Table S6 (detail) and Table 3 (summary). The ranges of mean leaf concentration for N, P and K were 39.3–44.4, 3.9–4.4 and 15.5–20.2 g kg^{-1} respectively, while for Ca and Mg they were 10.6–16.5 and 4.1–4.7 g kg^{-1} respectively (Table 2). Mu and Bu had higher mean leaf concentrations of S, Fe, Mn, Zn and Ni than Ru and Ki. The whole range of leaf Si concentrations was

0.7–14.1 g kg^{-1} , while mean values (4.4–5.5 g kg^{-1}) did not differ significantly between sites (Table 3). Most Al foliar levels were below 1 g kg^{-1} (Table S6). The range of leaf Al concentration was wider at Mu and Bu sites (0.2–6.5 g kg^{-1}) than at Ru and Ki sites (0.06–1.7 g kg^{-1}) (Table 3). Yet, the mean values of the leaf Al/Si ratio did not differ significantly from one site to another, although they were slightly lower in the Ru and Ki sites. The range of leaf Ge concentrations was 0–74 $\mu\text{g kg}^{-1}$ for Bu, Ru and Ki. It was particularly large in Mu foliar samples (8–738 $\mu\text{g kg}^{-1}$) (Table 3), the values measured for Mu6 and Mu7 being particularly high (Table S6). So, the range of Ge/Si ratio ($\mu\text{mol mol}^{-1}$) was 1.2–58.3, 0.6–5.9, 1.4–5.6 and 0.7–4.4 in Mu, Bu, Ru and Ki, respectively (Table S6), with respective mean values of 9.4, 1.5, 2.9 and 2.3 (Table 3).

Cassava phytoliths

Cassava phytoliths varied in size from about 2 to 50 μm (Fig. 4). They were of various morphotypes as defined in the International Code for Phytolith Nomenclature (Neumann et al. 2019): tabular and cylindrical elongate (Fig. 4a, 4f), tabular and spheroidal (Fig. 4c), spheroidal polylobate

Fig. 2 Concentration of CaCl_2 extractable Si ($\text{CaCl}_2\text{-Si}$) as plotted against the concentration of soil amorphous Si, as evaluated following DeMaster (1981) in 12 selected plots with 3 replicates, noting that ASi was measured in these 12 plots unlike $\text{CaCl}_2\text{-Si}$ (40 plots). Experimental data are reported in Table S4

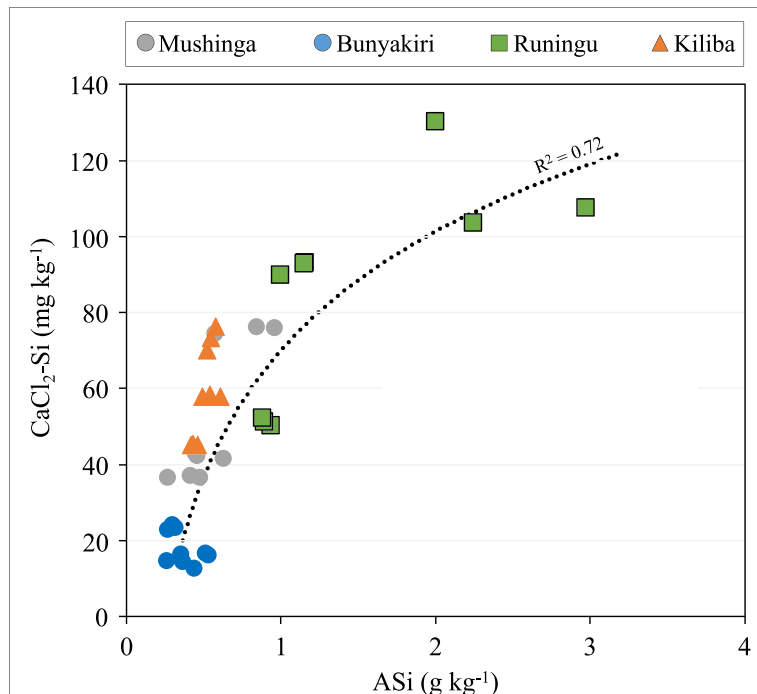
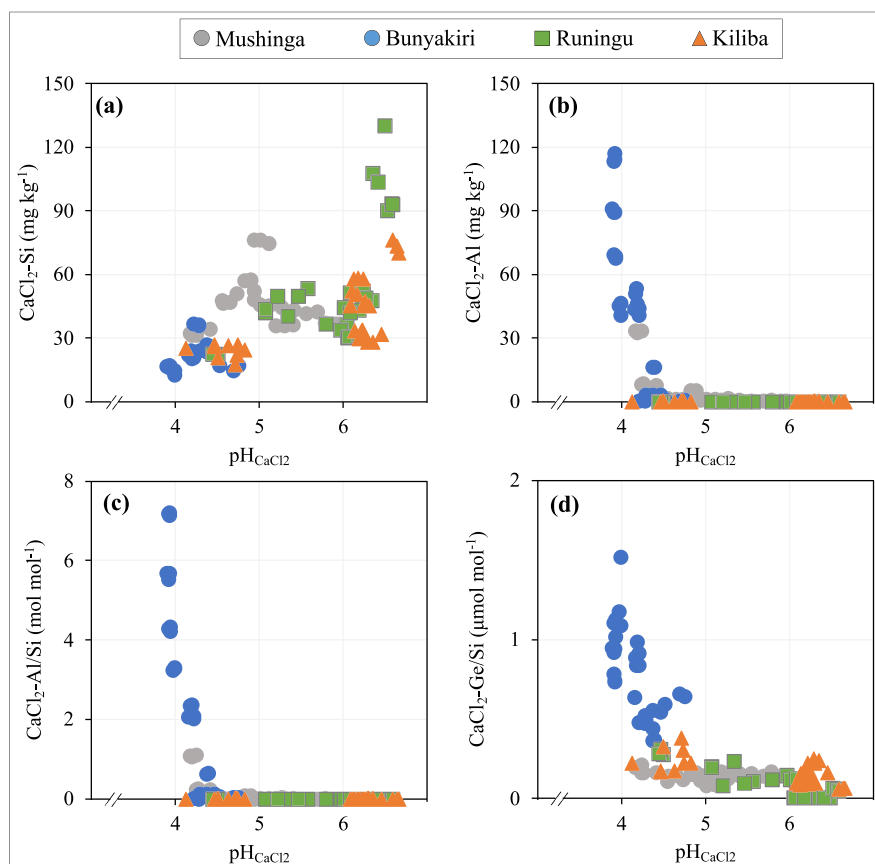


Fig. 3 (a–b) Concentrations of CaCl_2 extractable Si and Al, respectively CaCl_2 -Si and CaCl_2 -Al, as extracted from topsoils (40 samples, 10/site), plotted against the pH of the CaCl_2 extract ($\text{pH}_{\text{CaCl}_2}$). (c–d) Molar ratios Al/Si and Ge/Si in the CaCl_2 extracts, respectively CaCl_2 -Al/Si and CaCl_2 -Ge/Si, plotted against the pH of the CaCl_2 extract ($\text{pH}_{\text{CaCl}_2}$). Experimental data are reported in Table S2



(Fig. 4d), polyhedral facetate (Fig. 4b), nodular reniform (Fig. 4e). The EDX spectra maps of elements (Fig. 4g–j) confirmed the highly siliceous character of phytoliths and revealed the presence of Al in Ru (Fig. 4h). The comparison of Si, Al and Ge concentrations in leaves and phytoliths extracted from them (Table 4) showed a systematic decrease in the molar ratios Al/Si and Ge/Si. The range of phytolithic Ge/Si ratio was 0.65–5.94 and 0.11–1.83 $\mu\text{mol mol}^{-1}$ in leaves and phytoliths, respectively. From the leaf material to phytolith particle, the Ge/Si ratio decreased by 2.5 to 14 times, except for Ru6 (1.3).

Cassava root yield and leaf biomass, CMD incidence

Fresh cassava root yields ranged from 0.5 to 18 t ha^{-1} in the 360 plots (Table 5a). In the selected 40 plots, the ranges of fresh root yield and dry leaf biomass were 0.6–13 and 0.05–3 t ha^{-1} , respectively (Table 5b). For a given site, I_{CMD} did not differ between local and improved varieties (Fig. 5) except

in Ru. As expected, the incidence of CMD (I_{CMD}) was generally higher at low altitude levels (Ru, Ki), relative to highland sites (Mu, Bu). Whatever the variety, the mean I_{CMD} value (%) increased following the sequence Bu (8) > Mu (23) > Ru (36) > Ki (57) (Table 5b), revealing healthiest situations in highlands, particularly in Bunyakiri.

Disentangling the environmental and mineral predictors of cassava root yield

Structural Equation Modelling (SEMod) highlighted both the direct and indirect pathways influencing root yield (data in Table S7). While no management practice emerged as a driver of root yield for the whole data set (Fig. S1), the model inferring the responses to mineralomasses and altitude accounted for 33% and 26% of yield and I_{CMD} variations, respectively (Fig. 6a), with an adequate fit (Table 6a). Altitude did not significantly impact Si uptake. Yet, altitude had a strong, direct and negative influence (factor loading)

Table 2 Mean concentrations of selected nutrients (N, P, K, Ca, Mg, S, Fe, Mn, Zn, Ni, Cu) in cassava leaves collected in the 40 plots (10/site) 12 months after plantation (12 MAP) at harvest. Full data are given in Table S5

Site	N	P	K	Ca	Mg	S	Fe	Mn	Zn	Ni	Cu
	g kg ⁻¹										
Mu	range	3.04–7.08	7.24–36.58	5.85–20.59	3.08–9.07	0.51–2.53	0.22–5.21	0.08–0.66	0.04–0.17	0.01–0.15	0.01–0.02
	mean	4.41	20.19	10.61	4.11	1.03	1.03	0.28	0.08	0.03	0.01
	s.d	1.78	8.12	4.97	1.51	0.21	0.21	0.04	0.04	0.04	0.00
Bu	range	2.89–5.03	10.97–21.83	12.10–21.99	2.44–7.64	0.71–2.06	0.20–5.17	0.12–0.86	0.04–0.17	0.01–0.07	0.01–0.01
	mean	3.74	15.55	16.52	4.30	1.09	0.96	0.43	0.12	0.04	0.01
	s.d	0.72	3.51	3.62	1.54	0.43	1.96	0.20	0.02	0.02	0.00
Ru	range	2.98–5.00	15.55–21.59	7.18–20.02	2.87–6.17	0.18–1.15	0.14–1.21	0.08–0.17	0.03–0.10	0.01–0.02	0.01–0.01
	mean	3.88	18.77	11.97	4.67	0.45	0.48	0.10	0.05	0.01	0.01
	s.d	0.68	2.06	3.58	1.31	0.28	0.28	0.03	0.02	0.01	0.00
Ki	range	1.91–5.70	8.12–22.79	3.62–24.05	0.79–7.07	0.30–0.97	0.06–1.32	0.08–0.17	0.03–0.10	0.01–0.01	0.01–0.01
	mean	4.17	17.88	13.82	4.26	0.55	0.60	0.12	0.06	0.01	0.01
	s.d	1.09	4.15	5.35	1.60	0.22	0.46	0.03	0.02	0.00	0.00

on yield (-0.308*) and I_{CMD} (-0.439**), which in turn was directly and negatively impacted by Si mineralo-mass (-0.445**). The impact of altitude on I_{CMD} at 7 MAP was not straightforward (Fig. 7a) but confirmed that maximal I_{CMD} decreases with increasing altitude. The evolution of the disease as measured by the difference between the I_{CMD} values at 7 and 3 MAP indicated a similar trend (Fig. 7b). However, other factors should have impacted the expression of the CMD and its evolution (Fig. 7a-b). The impact of plant Si on root yield was obviously modulated by other factors, which were not site-specific characteristics (Fig. 7c). However, Si uptake impacted I_{CMD} , depending on altitude (Fig. 7d). The above observations led us to focus on the plant mineral predictors of cassava root yield (Fig. 6b). The final structural equation model accounted for 65% of yield variation ($R^2=0.65$, $p<0.01$) (Fig. 6b) with an adequate fit (Table 6b). Silicon uptake had the strongest direct influence (factor loading) on root yield (0.449), followed by CMD incidence (-0.143). In addition, Si had a direct negative link with CMD incidence (-0.249) as well as an indirect effect on it through the respective positive and negative influences of micronutrients (-0.249) and N (0.167) uptakes. Lastly, Si had direct positive links with the uptake of micronutrients (0.786) and N (0.703). In summary, the SEMod analysis indicated that Si mineralomass had both direct and indirect effects on CMD incidence and root yield.

Discussion

Soil bioavailable Si content covered a wide range revealing weak to strong soil desilication

The range of $CaCl_2$ -Si concentrations (13–130 g kg⁻¹, Fig. 2) matched that reported for a wide variety of soils (12–150 g kg⁻¹) as reviewed earlier (Fig. 12 Vander Linden et al. 2021). Since the dilute $CaCl_2$ extract mimics soil solution, this concentration range is consistent with lowest $CaCl_2$ -Si concentrations in Bu and highest $CaCl_2$ -Si concentrations in Ru topsoils. In line with literature data compiled earlier (Vander Linden et al. 2021), the ASi pool of the studied topsoils was a major source of bioavailable Si (Fig. 2), this pool encompassing both amorphous mineral silicates and biogenic silica particles, phytoliths (Cornu et al. 2022; Li et al. 2022) or possibly

Table 3 Mean values, range and standard deviation (s.d.) for the concentrations of Si, Al, and Ge and the molar ratios Al/Si and Ge/Si in cassava leaves collected in the 40 plots 12 MAP at harvest (10 plot per site)

		Si	Al	Ge	Al/Si	Ge/Si
Site		(g kg ⁻¹)	(g kg ⁻¹)	(μg kg ⁻¹)	(mol mol ⁻¹)	(μmol mol ⁻¹)
Mu	range	2.06–14.11	0.23–6.38	8.62–738.35	0.09–0.47	1.24–58.34
	mean	4.46	1.13	146.51	0.19	9.40
	s.d	3.76	1.88	274.07	0.12	18.13
Bu	range	2.10–13.01	0.20–6.52	0.00–74.52	0.00–0.52	0.00–5.94
	mean	5.51	1.18	19.87	0.18	1.55
	s.d	4.14	1.94	23.17	0.15	1.72
Ru	range	1.90–7.74	0.16–1.57	7.20–70.04	0.09–0.18	1.46–5.58
	mean	4.63	0.63	34.46	0.13	2.95
	s.d	2.14	0.40	18.51	0.03	1.37
Ki	range	0.70–8.22	0.06–1.71	7.70–58.80	0.09–0.22	0.71–4.44
	mean	5.05	0.78	29.75	0.14	2.35
	s.d	2.46	0.59	20.51	0.05	1.15

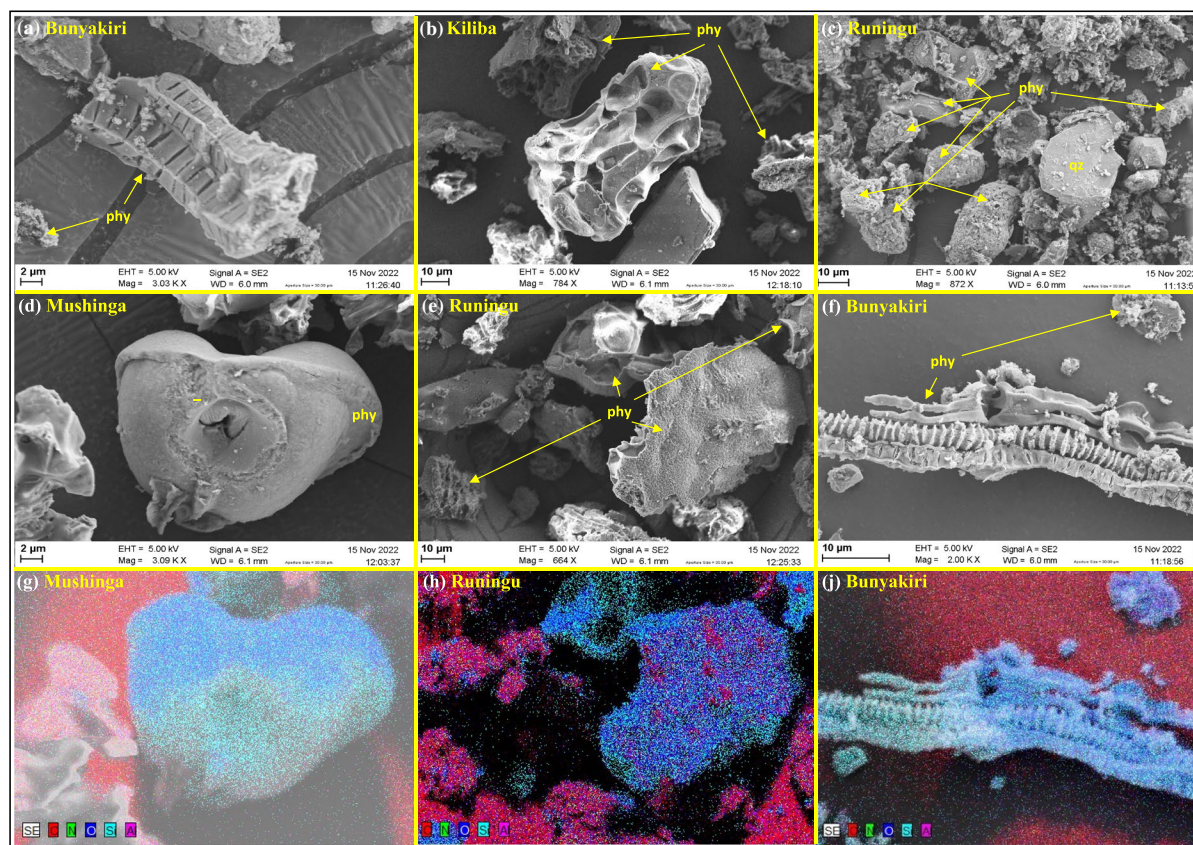


Fig. 4 SEM images of cassava phytoliths extracted after leaf dry ashing: (a–f) images illustrate the variability of phytolith morphology in cassava plant; (g–j) the EDX spectra maps of

elements (Si, O, C, Al) (g), (h) and (j) correspond to the SEM images (d), (e) and (f), respectively

Table 4 Concentrations of Si, Al and Ge in 12 selected leaf and phytolith materials, as extracted by dry ashing, with the corresponding values of the molar ratios Al/Si and Ge/Si

Plot	Leaf					Phytolith				
	Si	Al	Ge	Al/Si	Ge/Si	Si	Al	Ge	Al/Si	Ge/Si
	g kg ⁻¹		µg kg ⁻¹	mol mol ⁻¹	µmol mol ⁻¹	g kg ⁻¹		µg kg ⁻¹	mol mol ⁻¹	µmol mol ⁻¹
Mu4	4.02	1.35	30.80	0.35	2.95	317.86	11.86	746.52	0.03	0.90
Mu8	2.72	0.23	8.73	0.09	1.24	152.61	2.37	83.84	0.01	0.21
Mu10	7.56	1.14	46.08	0.16	2.35	252.31	9.43	357.77	0.03	0.54
Bu3	3.55	0.32	12.08	0.09	1.31	54.60	1.91	76.68	0.03	0.54
Bu4	9.12	0.36	15.42	0.04	0.65	321.75	3.06	94.01	0.01	0.11
Bu8	4.83	1.84	74.52	0.39	5.94	313.51	15.41	664.18	0.05	0.82
Ru1	4.84	0.63	70.04	0.13	5.58	83.43	4.98	318.38	0.06	1.47
Ru6	5.03	0.50	32.28	0.10	2.47	37.48	2.17	178.27	0.06	1.83
Ru7	1.90	0.16	7.20	0.09	1.46	27.85	1.12	37.53	0.04	0.52
Ki5	7.86	1.71	50.87	0.22	2.49	249.26	5.65	310.95	0.02	0.48
Ki6	4.20	0.34	7.70	0.09	0.71	136.91	3.34	83.75	0.02	0.23
Ki7	0.70	0.06	8.12	0.09	4.44	134.48	4.80	110.83	0.03	0.31

Table 5 Mean values with standard deviation (s.d.) and ranges for cassava fresh root yield and dry leaf biomass measured 12 MAP at harvest, and CMD incidence (I_{CMD}) measured 7 MAP (**a**) in the 360 plots and (**b**) in the selected 40 plots (10/site)

Site	Root yield (t ha ⁻¹)		Leaf biomass (t ha ⁻¹)		I_{CMD} at 7 MAP (%)	
(a)	mean (s.d.)	range	mean (s.d.)	range	mean (s.d.)	range
Mu	3.02 (0.23)	0.46–18.48	0.93 (0.05)	0.05–3.02	23.15 (16.8)	0–78
Bu	6.50 (0.34)	0.53–17.41	0.81 (0.04)	0.11–2.26	8.85 (9.54)	0–67
Ru	4.48 (0.46)	0.89–13.84	0.99 (0.14)	0.25–5.02	43.15 (33.77)	0–100
Ki	3.81 (0.32)	0.58–13.57	0.69 (0.06)	0.05–2.34	43.67 (32.66)	0–100
(b)						
Mu	2.85 (0.90)	0.92–10.38	1.15 (0.35)	0.05–3.02	23.05 (15.84)	0–47
Bu	5.63 (1.28)	0.64–12.98	0.75 (0.11)	0.28–1.25	7.68 (8.11)	0–25
Ru	3.09 (0.53)	0.89–5.02	0.70 (0.10)	0.26–1.32	36.24 (32.77)	0–91
Ki	3.86 (0.99)	0.72–10.94	0.86 (0.24)	0.05–2.34	57.09 (27.97)	5–100

micrometric water-soluble silica particles (Puppe et al. 2017). Deciphering the source of aqueous Si ($\text{CaCl}_2\text{-Si}$) can be achieved using the Al/Si and Ge/Si ratios of aqueous extracts (Li et al. 2022). The low $\text{CaCl}_2\text{-Al/Si}$ and -Ge/Si ratios, below 0.5 mol mol⁻¹ and 0.3 µmol mol⁻¹, respectively (Fig. 3c-d and Table S2), showed that phytoliths were the major source of bioavailable Si in Mu, Ru and Ki topsoils. In contrast, aqueous Si was likely released from fine-sized disordered kaolinite in Bu topsoils as indicated by higher $\text{CaCl}_2\text{-Al/Si}$ and -Ge/Si ratios (Li et al. 2022). These results revealed the instability of kaolinite in dilute solution, hence supporting strong desilication in Bu soils. Besides, they were consistent with the preferred dissolution of kaolinite at $\text{pH}_{\text{CaCl}_2}$ below

4.5 (Li et al. 2022) and that of phytoliths at $\text{pH}_{\text{CaCl}_2}$ above 6 (Frayssé et al. 2009; Meunier et al. 2018). The release of bioavailable Si depends on both the nature of the source component and pH (Cornu et al. 2022; Frayssé et al. 2009; Haynes 2019; Keller et al. 2021; Li et al. 2022; White et al. 2012). The substantial release of Al in Mu topsoils (Fig. 2b) could originate from poorly crystalline gibbsite (Vander Linden et al. 2021).

Improved varieties and CMD incidence

As shown above in Fig. 5, the “improved variety” did not discriminate our cassava plots in terms of CMD incidence. This may seem surprising since

Fig. 5 Box plots illustrating the incidence of cassava mosaic disease (ICMD), as measured 7 MAP for local and improved varieties in 360 plots distributed in the four sites as follows: 120 (Mushinga), 120 (Bunyakiri), 47 (Runingu), 73 (Ki). Local varieties have been used for years by several farmers' generations while improved varieties are delivered by external organizations for various purposes, not exclusively for disease tolerance (see our text in Discussion)

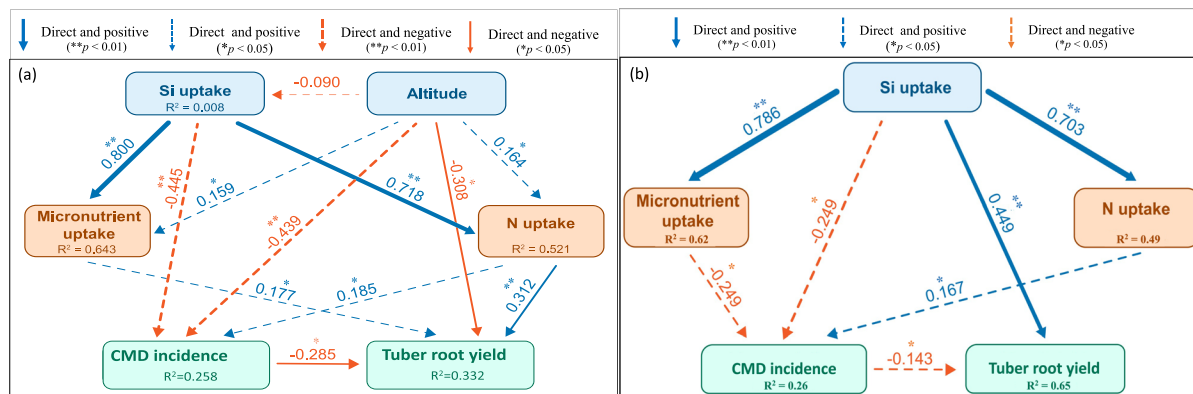
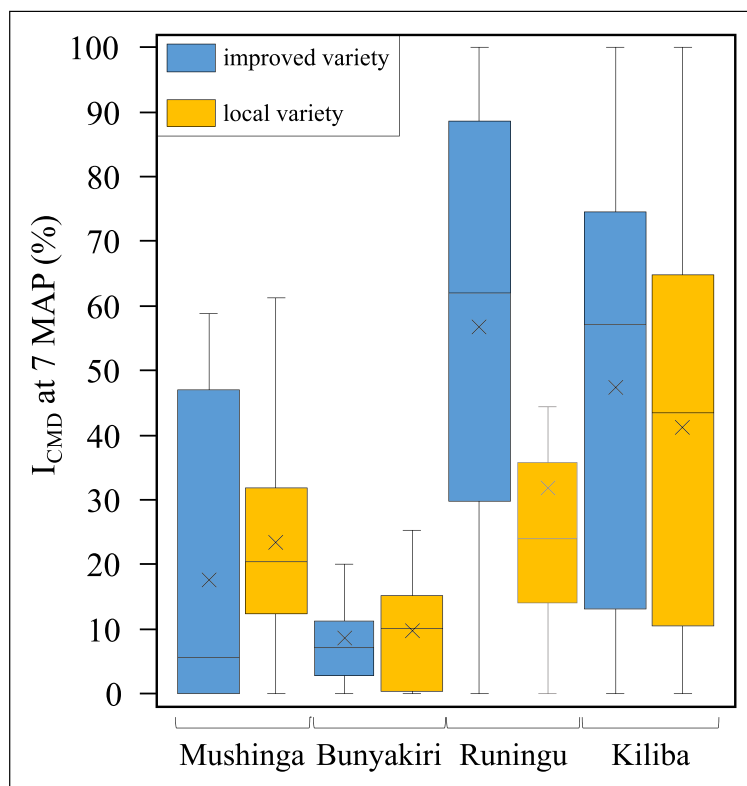


Fig. 6 Structural Equation Model (SEMod) with two scenarios. **(a)** SEMod of altitude and Si uptake impacts on CMD incidence at 7 MAP (ICMD-7MAP) and cassava root yield. **(b)** SEMod of Si uptake impact on ICMD-7MAP and cassava root yield. The asterisks indicate the statistical significance level based on p values: * $p < 0.05$, ** $p < 0.01$. All the paths were significant, except in (a) for the link altitude-Si uptake. Factor loadings are indicated for each path: the numbers adjacent to the lines are the standardized path coefficients, indicating the

degree of standard deviation changes in dependent variables if each of the independent variables change by one standard deviation. The blue and red lines represent positive and negative effects, respectively. The line width is proportional to the strength of the standardized path coefficient. N uptake means nitrogen uptake. Micronutrient uptake sums up the uptakes of Fe, Mn, Zn and Cu. The model had a good fit based on each of the goodness-of-fit criteria (Table 6)

Table 6 Indicators of the goodness-of-fit for the final SEM in each step of the final model construction: root mean squared error of approximation (RMSEA); comparative fit index (CFI);

Core SEMod	RMSEA	CFI	GFI	χ^2	P	df	R ²
(a) with altitude	0.000	1	0.995	0.520	0.914	3	0.33
(b) without altitude	0.000	1	0.990	2.208	0.530	3	0.65

goodness-of-fit index (GFI), model chi-square (χ^2), *P* value, degree of freedom (df), adjusted R². The indicators are given for two scenarios (a) with and (b) without altitude response

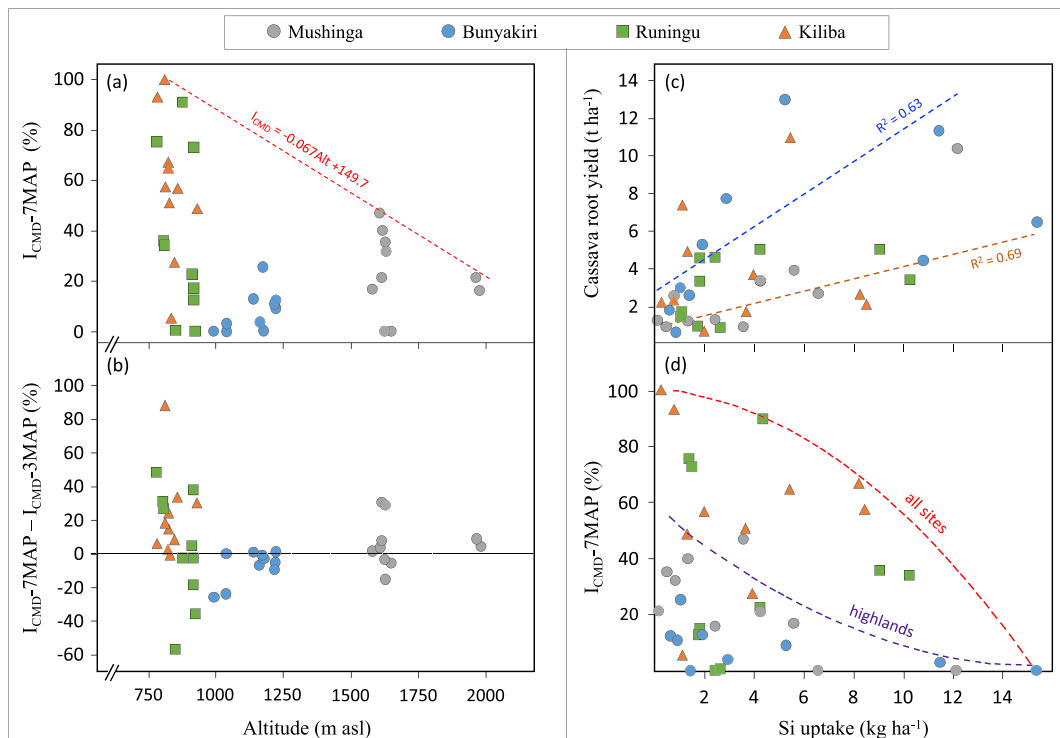


Fig. 7 (a–b) Impact of altitude on (a) the CMD incidence as measured 7 months after plantation (ICMD-7MAP) and (b) the difference between the values of ICMD measured 7 and 3 MAP (ICMD-7MAP – ICMD-3MAP). The difference (ICMD-7MAP – ICMD-3MAP) is considered as a marker of the evolution of the disease. (c–d) Impact of Si uptake by cassava plant (product of leaf biomass with Si concentration), as measured 12 MAP in 40 selected plots (10/site) on (a) root yield and (b) ICMD-7MAP. (c) For the whole set of data, the value of R²

was 0.23. Two populations of identical weight ($n=20$) were distinguished (P1, P2). For each population, R² significantly increased (P1: 0.63; P2: 0.69), with a stronger impact of plant Si on root yield in P1 than in P2. (d) The maximal ICMD-7MAP value decreased significantly with increasing Si uptake. However, ICMD was mediated by altitude since at given Si uptake, maximal ICMD was much lower in highlands (Mu, Bu) than in all sites

improved varieties can be associated with disease resistance, as commonly considered. Searching for resistance to CMD in cassava has a long history as the disease strongly depresses crop yield (Hahn et al. 1980). However, though positive relationships were established between the extent and severity of the leaf symptoms and yield loss, losses can be considerable, even with improved varieties designated

as resistant (Thresh et al. 1994). Actually, wild cassava species (*Manihot glaziovii*) can exhibit lower infection degrees by CMD viruses than improved cultivars (*Manihot esculenta* Crantz) (Ambang et al. 2007), while cassava resistance to viral diseases covers a large spectrum in terms of plant responses (Sheat and Winter 2023). In addition, in South-Kivu, the improved cassava varieties were introduced for

several characters, not only plant resistance as mentioned in the section Materials and Methods.

Silica accumulation in cassava leaves is similar to that of macronutrients and forms phytoliths of various morphotypes

Foliar concentrations of plant nutrients varied greatly between farm plots (Table S5). Nutrient levels did not indicate any deficiency or excess according to the standards available for foliar diagnosis in cassava (Howeler 2002; Reuter et al. 1997) except for nitrogen (N) and sulfur (S). Indeed, leaf N concentrations ($39\text{--}44\text{ g kg}^{-1}$, Table 2) were below the $50\text{--}65\text{ g kg}^{-1}$ range defined for adequate N nutrition (Reuter et al., 1997). On the other hand, leaf S concentrations ($0.18\text{--}2.53\text{ g kg}^{-1}$) were below the adequate level evaluated at 2.7 g kg^{-1} at 3–4 MAP by Howeler (2002). Yet, no S deficiency was noted in the field, while S uptake had no impact on CMD incidence and root yield. Nutrient concentrations can vary considerably among plant parts and change during the growth cycle (Howeler 2002). Though Si is not a plant nutrient (Coskun et al. 2019), Si concentration in cassava leaves varied from 2.1 to 14.1 g kg^{-1} (Table 3) in a range similar to that of plant macronutrients (Table 2), regardless of soil type. The uptake of Si by cassava did not vary with variety type (Fig. S1), soil weathering stage nor desilication degree, unlike for banana (Henriet et al. 2008) or rice (Klotzbücher et al. 2015; Li et al. 2020). Banana, in its vegetation phase, and rice have a shorter cycle than cassava. Besides, their roots develop mainly in the topsoil (upper 30 cm) (Delvaux 1995; Yoshida and Hasegawa 1982), while for cassava the rooting depth is much greater ($1\text{--}2.5\text{ m}$) (Gregory and Wojciechowski 2020), implying that Si can be taken up from a larger soil volume. In addition to rooting depth, management practices impact the Si soil–plant cycle (Vander Linden and Delvaux 2019). This cycle might thus have been influenced in the studied farms by soil and soil fertility management, soil cover, weed control, recycling or export of plant parts, and intercropping (Table S8). As mentioned in the section Materials and Methods, the impact of management practices is being analyzed elsewhere. Yet, our current analysis indicates a strong conditionality of the effect of any given practices, while none of them appears as a

driver, direct or indirect, of root yield for the whole set of plots.

Cassava leaves formed fine-sized phytoliths of various morphotypes (Fig. 4), which may contain Al (Fig. 4h and Table 3). The low range of leaf Al/Si ($0\text{--}0.52$) excluded clay dust contamination (Table 4). Both Al/Si and Ge/Si ratios were used to trace Si in soil–plant systems (Li et al. 2022). However, though Al concentrations in plant phytoliths cover a substantial range ($0.6\text{--}9\text{ g kg}^{-1}$) (Bartoli 1985; Buján 2013; Frayse et al. 2009; Hodson 2016), the Al/Si is little used to characterize phytoliths, unlike the Ge/Si ratio. Being analog to Si, the variation in Ge concentration follows that of Si in ecosystems (Wiche et al. 2018). Germanium concentrations measured in cassava leaves were within the range of values available for other field-grown plants, most being below $85\text{ }\mu\text{g kg}^{-1}$ (Table 7). The same applies to the Ge/Si ratio in both leaf and phytolith material. The sharp and systematic decrease in Ge/Si ($\mu\text{mol mol}^{-1}$) from leaf ($0.65\text{--}5.94$) to phytolith ($0.11\text{--}1.83$) (Table 4) indicated that Ge accumulation in cassava leaves was not solely driven by its incorporation in phytoliths as reported in other plant species (Kaiser et al. 2020). Actually, Ge and Si follow different pathways in plant tissues (Delvigne et al. 2009; Kaiser et al. 2020; Sparks et al. 2011) due to the higher reactivity of Ge with many organic functional groups (Wiche et al. 2018).

Silicon uptake enhanced cassava root yield and reduced CMD incidence

As previously noted in South-Kivu, cassava root yields (Table 4) were low to extremely low ($0.5\text{--}18\text{ t ha}^{-1}$), far below the yield potential of $75\text{--}90\text{ t ha}^{-1}$ (Cock et al. 1979; Fermont et al. 2009) due to major biotic and abiotic constraints as well as poor logistic, socioeconomic and institutional context (Cirimwami et al. 2019; Munyahali et al. 2017; Ouma et al. 2011; Pypers et al. 2011). Actually, Si had a pivotal role on cassava root yield in the studied farms (Fig. 6b). Well-known in monocots, Si accumulation also occurs in some dicot species (Hodson et al. 2005), with direct positive effects on plant biomass, crop yield and stress tolerance (e.g., Belanger et al. 1995; Pereira de Souza Junior et al. 2019; Parecido et al. 2022; Shamshiripour et al. 2022). As illustrated in Fig. 7c, the direct influence of Si uptake on cassava

Table 7 Some examples of Ge concentrations in plant tissues (shoot, leaf) and phytoliths from different field-grown plants, unless otherwise indicated, compared to those measured in cassava in this study

Plant functional group and/or species	plant part, phytolith	Ge $\mu\text{g kg}^{-1}$	Ge/Si $\mu\text{mol mol}^{-1}$	Reference
Banana, <i>Musa acuminata</i>	leaf	0.8–5.1	0.16	Delvigne et al. 2009
Grass, <i>Oryza sativa</i>	shoot	2900		Wiche et al. 2018*
various <i>Poaceae</i>	shoot	37–450		''
(monocots)	leaf	22–55		''
	leaf	67–330	10.14–38.03	Kaiser et al. 2020
	phytolith	500–800	0.83–1.95	''
hydroponic study	leaf	0.02–0.05	0.04–0.12	Blecker et al. 2007
	phytolith	0.03–.004	0.07–0.10	''
Forb (various dicot species)	shoot	8–50		Wiche et al. 2018*
	leaf	8–310		''
<i>Equisetum</i> sp.	shoot	20		''
	leaf	10–210	0.06–0.77	Delvigne et al. 2009
Tree (coniferous)	needle	1–3	0.10–1.50	Cornelis et al. 2010
Tree (broadleaf)	leaf	4–84	0.20–0.30	''
Cassava (<i>Manihot esculenta</i>)	leaf	7.2–74.5	0.71–5.94	This study (Table 4)
	phytolith	37–746	0.11–1.83	''

* Wiche et al. 2018, and references therein

root yield presumably reflected the benefits of Si for cassava grown under multi-stress conditions, as it occurs in many plants (Coskun et al. 2019; Rodrigues et al. 2015). Plotting root yield against leaf Si concentration gives very similar relationship (not shown). The impact of Si on root yield (Fig. 7c) has been modulated by other factors while the emergence of two populations indicated that the response to Si depends on several factors, not identified here. It is not related to the use of improved varieties. Yet, other management practices could possibly be involved, but this is beyond the scope and size of the present study. The direct impact of Si on N and micronutrient uptake was expected given the effectiveness of Si in improving mineral nutrition in many plant species (Rodrigues et al. 2015), notably N and micronutrients (e.g., Cuong et al. 2017; Etemasi and Jeong 2018; Hong et al. 2022). The influence of Si on root yield was also indirect since CMD incidence negatively affected yield while being itself negatively influenced by Si (Fig. 6b). The direct effect of Si on CMD incidence was evidently modulated by altitude (Fig. 7a–d), as reported earlier (Bisimwa et al. 2019; Macfadyen et al. 2018), but also by other factors (Fig. 7d). The negative effect of Si on CMD incidence (Fig. 6a–b) was consistent with known facts about the action and role of Si in enhancing plant resistance against insect pests and fungal diseases (Coskun et al. 2019;

Fauteux et al. 2005), and bacterial infections (Islam et al. 2020; Sakr 2016), Si acting as an extracellular prophylactic agent against stresses (Coskun et al. 2019). However, the role of Si in relation to viral pathogens attracted little attention (Islam et al. 2020; Rodrigues et al. 2015; Sakr 2016). Silicon-modulated protection against viral infection occurred through a specific defence mechanism in tobacco (Zellner et al. 2011) and by limiting or inhibiting the virus transmission by insect in rice (Jia et al. 2021). Aqueous H_4SiO_4 and silica nanoparticles induced systemic acquired resistance (SAR) in *Arabidopsis* through triggering salicylic acid (SA), the plant hormone responsible for the activation of pathogenesis-related (PR) genes (El-Shetehy et al. 2021). Interestingly, SA played a crucial role in regulating antiviral mechanisms in some cassava cultivars (Malichan et al. 2023) while PR gene families revealed responses to whitefly infestation and SA in cassava (Garceau 2021; Irigoyen et al. 2020). Thus, the direct negative link between plant Si and I_{CMD} can hypothetically involve the impact of Si uptake by cassava on both the vector (*Bemisia tabaci*) and the viral pathogen. Silicon had also indirect influences on CMD incidence through the uptake of micronutrients and N (Fig. 6b). Micronutrients play specific roles in improving plant tolerance to diseases (Datnoff et al. 2007; Dordas 2008). Nitrogen is involved in plant responses via complex

host–pathogen interactions (Dordas 2008), which often increase disease susceptibility (Ballini et al. 2013). Generally, it has negative effects on physical defences and production of antimicrobial phytoalexins, but positive ones on defence-related enzymes and proteins (Sun et al. 2020). The decrease in I_{CMD} at higher Si and lower N uptake (Fig. 6b) suggested that the N:Si balance may have affected plant tolerance to CMD. However, our data set revealed no significant trend in the relationship between N:Si balance and I_{CMD} . In rice, optimizing the N:Si balance increased grain yield and lodging resistance (Hong et al. 2022), and decreased N-induced susceptibility to blast disease, the expression of which was modulated under earthworm-silicon control (Blanchart et al. 2020). Little is known about the impact of N on viral plant diseases. A high N supply enhanced the infection of cotton by the leaf curl virus (Zafar et al. 2010) while higher leaf C:N ratio delayed viral damage in tobacco (Ye et al. 2010). Yet, *Rhizobium* inoculation enhanced plant vigor and systemic resistance to the mosaic virus in faba bean (Abdelkhalek et al. 2022). Further investigation under controlled conditions can help unravelling such potential effects in cassava.

Silicon uptake alleviated soil acidity stress

Most likely in our case study, other factors interplayed to modulate the impacts of Si on cassava performance since Si accumulation in plants also mitigates abiotic stresses. The reputed tolerance of cassava to soil infertility (Howeler 2002) and its significant response to fertilization (Fermont et al. 2010) indicates the existence of adaptive mechanisms. Cassava is renown to be tolerant to soil acidity (Howeler 2002), but large differences in this respect exist between cultivars (Edwards and Kang 1978; Lozano et al. 1981; Manrique 1985; Nassar 2000; Punpom et al. 2022; Spain et al. 1975). Soil acidity enhances the bioavailability of toxic Al. In our field-sampled cassava leaves, the range of Al concentrations was 0.06–6.52 g kg⁻¹ (Table 3), but all values except one were below 3 g kg⁻¹ (Table S6: 0.06–1.84 g kg⁻¹). Foliar levels above 3 g kg⁻¹ denoted Al hyperaccumulation, which occurs in some *Euphorbiaceae* (Jansen et al. 2002). The range observed here was higher than 0.005–0.63 g kg⁻¹ measured in 400 cassava genotypes tested in two soils (Alamu et al. 2022) as well as 0.05–0.13 g kg⁻¹ in two cassava cultivars in

a sand-hydroponic experiment (Punpom et al. 2022). In this controlled experiment, high Al levels up to 2–2.5 mg l⁻¹ in the nutrient solution enhanced proton release by cassava roots, hence favoring mineral dissolution in the rhizosphere while Al levels up to 1.35 mg l⁻¹ increased Fe acquisition by roots, thus elaborating on the beneficial role of Al in mineral uptake by cassava (Punpom et al. 2022). Interestingly, in our data set (40 plots), Al concentration in cassava leaves was strongly correlated with that of Fe ($r=0.99$). In addition, it was also directly related to the foliar level of Si ($r=0.84$), suggesting a possible role of Si in alleviating Al toxicity as reported in maize (Wang et al. 2004) and recently reviewed for several plant species (Hodson and Evans 2020). However, the question of whether Si accumulation in cassava could be an adaptive mechanism enabling the plant to grow on poor acid soils remains open in terms of mechanisms.

A perspective to enhance Si uptake by cassava in farming systems

The integrated soil fertility management (ISFM) has been successfully applied in cassava cropping systems in the studied area (Munyahali et al. 2017; Pypers et al. 2011). It is defined as a set of practices including the use of fertilizer, organic input and improved germplasm, as adapted to local conditions to maximize their agronomic efficiency and improve crop productivity (Vanlauwe et al. 2010). Given that mineral Si fertilizers are costly, poor in soluble Si and not available locally, using biomass residues would offer promising perspectives. Using organic residues to enhance the effective supply of bioavailable Si could be practically done through amending soils with biochar. The use of biochar as a Si input indeed offers undeniable potential to mitigate desilication and to enhance the effect of Si in alleviating plant stresses (Li and Delvaux 2019), knowing that relevant trade-offs for climate change mitigation exist between biochar production and its application to soil (Lehmann et al. 2021). The potential of biochar is significant in contributing to ISFM and climate-smart agriculture, as shown in farming systems of Uganda (Roobroeck et al. 2019) and Kenya (Kätterer et al. 2019). Improving the bioavailability of Si in soils can also be achieved by recycling crop residues (Marxen et al. 2016; Puppe et al. 2021; Yang et al. 2020).

Conclusion

Our study shows that Si accumulated substantially in cassava leaves, where it formed phytoliths of different morphotypes. In addition, our work indicates that Si mineralomass was a predictor of cassava root yield through both direct and indirect pathways. Importantly, the indirect pathways involved well-known impacts of Si and micronutrients on disease tolerance in other plant species. Moreover, our data also suggest a contribution of Si to cassava tolerance to soil acidity and Al stress. Although our observational study cannot fully disentangle causal relationships, our results highlight the potential unknown role of Si in cassava productivity while opening new avenues of research. These should ideally consider the role of Si in the interactions between host, cassava viruses and their insect vectors, as well as in the plant tolerance to soil infertility and water stress, all of which are major constraints to cassava productivity.

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Author contributions FB designed the field study and was guided by BV and BD. FB carried out the field sampling, with the IITA support and assistance of BD. BD and ZL designed the laboratory studies. BD, ZL and FB processed, analyzed and treated field and laboratory data. CB analyzed the CMD data and improved their interpretation. BD and ZL piloted the data interpretation and BD the manuscript writing.

Data availability Our experimental data can be available on request.

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