

OIKOS

Research article

Effects of plant-available soil silicon on seedling growth and foliar nutrient status across tropical tree species

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Oikos

2023: e10030

doi: [10.1111/oik.10030](https://doi.org/10.1111/oik.10030)

Subject Editor: Richard Michalet

Editor-in-Chief:

Gerlinde De Deyn

Accepted 19 March 2023



Plant-available silicon (Si) concentrations vary considerably across tropical soils, yet the ecological importance of that variation remains largely unresolved. Increased Si availability can enhance growth and modulate foliar nutrient status in many crop species suggesting similar effects might occur in natural systems. However, how growth, foliar Si and macronutrient concentrations as well as their stoichiometry respond to plant-available Si and how these responses differ across tropical tree species is unknown. We experimentally exposed seedlings of 12 tropical tree species to a gradient of plant-available Si concentrations, representing 85 % of the variation found across central Panama, and assessed responses in aboveground growth and foliar nutrient status. Furthermore, we assessed whether higher plant-available Si increases P availability. Increasing plant-available Si led to increased foliar Si concentrations (by up to 140%). It also led to higher aboveground growth (by up to 220%), and it affected foliar C and N concentrations, and nutrient stoichiometry across species. However, at the species-level only a small subset of two to four species showed significant growth and foliar nutrient responses. At the soil-level, plant-available P remained unchanged along the experimental soil Si gradient. Our results showed that Si can improve growth and/or modulate foliar nutrient status in a number of tropical tree species. Furthermore, species' growth and foliar nutrient concentrations might vary differently across tropical forest sites varying in plant-available Si. Additionally, Si-induced responses in foliar nutrient stoichiometry have the potential to affect herbivory and litter decomposition. Taken together, natural variation in plant-available Si might influence plant performance unequally across tropical tree species, and change trophic interactions, with potential implications for ecosystem processes.

Keywords: interspecific variation, nutrient stoichiometry, phytolith, plant nutrition, plant-soil interactions, trait plasticity



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Introduction

Plants require nitrogen (N), phosphorus (P) and carbon (C) to maintain protein production, photosynthesis and growth (Lambers and Oliveira 2019). Their foliar concentrations and stoichiometric ratios govern important ecological processes, including herbivory and litter decomposition (Poorter et al. 2004, Coley et al. 2006, Cornwell et al. 2008), and any changes in these concentrations or ratios can have pronounced consequences at the individual, species and community level. Foliar macronutrient concentrations and their stoichiometry are physiologically, biochemically and genetically constrained (Elser et al. 2010), yet they respond plastically to environmental factors, such as changing soil chemistry (Reich and Oleksyn 2004, Mayor et al. 2014). The availability of Si to plants has also been shown to modulate foliar nutrient status, to promote biomass production and to alleviate multiple abiotic and biotic stressors (Cooke and Leishman 2016, Neu et al. 2017, Frew et al. 2018, 2019, Greger et al. 2018). Such effects of Si have been studied primarily in agricultural species, where Si fertilization is widely used to improve plant performance and resilience (Cooke and Leishman 2011). Yet, potential effects of Si on plant growth and foliar nutrient status remain understudied in natural systems, such as tropical forests.

Tropical forests display a remarkable tree species diversity exhibiting pronounced variation in foliar chemistry (Hättenschwiler et al. 2008, Wright 2019). Recent studies demonstrated that concentrations of plant-available Si vary considerably in tropical soils, and that trees show pronounced inter- and intraspecific variation in foliar Si concentrations (Schaller et al. 2018, Ishizawa et al. 2019). Maximum foliar Si concentrations in these trees were similar to those of high-accumulating grass species (Ma and Yamaji 2006), which have long been the main focus of Si research (Cooke and Leishman 2011). The ecological consequences of variation in plant-available and foliar Si might be pervasive considering that Si can alleviate important stressors that shape species performance and distribution in tropical forests, such as P limitation (Condit et al. 2013, Wright 2019), herbivory (Eichhorn et al. 2010, Bagchi et al. 2014) and drought (Engelbrecht et al. 2007, Condit et al. 2013). To advance our understanding of the ecological role of Si in tropical forests, we need to elucidate the responses of plant growth, foliar Si and macronutrient concentrations as well as stoichiometry to plant-available Si, and how responses differ across species.

Plant roots take up Si as dissolved mono-silicic acid from the soil. Then, Si is carried to aboveground organs with the transpiration stream, where it accumulates and forms amorphous Si deposits (Raven 1983, Ma and Yamaji 2006). In most species and under experimental conditions higher plant-available Si routinely led to increased foliar Si concentrations (Liang et al. 2006, Neu et al. 2017, Greger et al. 2018, Klotz et al. 2021). The contributions of different Si uptake mechanisms, i.e. active Si uptake by transporters versus passive uptake by diffusion, vary across species and determine their capacity to take up Si and to respond to plant-available Si (Liang et al. 2006, Deshmukh and Bélanger 2016). Indeed, in temperate herbaceous species,

the ability to respond to plant-available Si was related to the physiological capacity for Si uptake, with stronger responses in species with higher Si uptake capacity (Klotz et al. 2021). As with previous studies, tropical tree species with high Si uptake capacities should show stronger foliar Si responses to increasing plant-available Si.

Performance-enhancing effects of increased plant-available Si were reported across species and families showing a wide range of Si uptake capacities (Cooke and Leishman 2016, Frew et al. 2018). They can result either from altered physiological and/or soil processes. Si fertilization has been shown to improve several physiological parameters, including photosynthesis, nutritional status and antioxidant activity (reviewed by Frew et al. 2018). Yet, the mechanistic interactions between these physiological parameters and Si, and how they influence growth, are far from clear (Coskun et al. 2019). Alternatively, Si-induced changes in soil processes might be the reason for the enhanced growth observed. For instance, dissolved mono-silicic acid has been shown to increase plant-available P by displacing inorganic P from binding sites on soil minerals (Schaller et al. 2019, 2020b). Work on tropical soils in Panama showed a positive correlation between plant-available Si and P, suggesting that a similar mechanism may exist in the tropics (Schaller et al. 2018), yet experimental evidence is missing.

Tropical trees should be particularly responsive to Si-induced increases in plant-available P, which is generally low in tropical soils, making P limitation of tree growth pervasive (Vitousek et al. 2010, Mayor et al. 2014, Wright 2019). However, the strength of foliar P and growth responses varies considerably across species (Mayor et al. 2014, Zalamea et al. 2016), which is attributed to their diverse array of P uptake strategies (Zalamea et al. 2016). For instance, species associated to P-poor soils invest substantial energy into foraging and mining strategies to access chemically unavailable forms of soil P (Reichert et al. 2022). As a result, in these species, foliar P and growth responses to Si-induced increases in plant-available P should be weak (Zalamea et al. 2016). By contrast, species associated to P-rich soils rely entirely on plant-available P and should exhibit a stronger Si-induced increase in foliar P concentrations and growth as well as decrease in foliar N:P ratios (Mayor et al. 2014, Zalamea et al. 2016).

Besides potential interactions between Si and P, Si can also influence foliar C concentrations. Negative correlations between plant C and Si concentrations within species have been shown in many field and experimental studies (reviewed by Hodson and Guppy 2022). Substitution of C-based compounds (e.g. lignin and phenols) by metabolically cheap and functionally equivalent Si deposits is a widely held, yet still controversial, explanation for that pattern (Cooke and Leishman 2011, reviewed by Hodson and Guppy 2022). In this way plants may allocate more C into growth and reproduction (Raven 1983), which should particularly benefit species in low resource environments (Quigley et al. 2020). Seedlings of tropical tree species are strongly limited by light, nutrients and occasional droughts in the forest understory (Engelbrecht et al. 2007, Rüger et al. 2009, Vitousek et al.

2010), and thus should benefit from Si substitution of C-based compounds. If Si substitutes C in tropical seedlings, increasing plant-available Si should lead to reduced foliar C concentrations with parallel changes in foliar C:N and C:P ratios. The responses in foliar Si and C should be coupled, so that species with stronger increases in foliar Si concentrations should show more pronounced decreases in foliar C concentrations.

Up to now, most experimental studies on how plant-available Si influences growth and foliar nutrient status focussed on single species, mostly grasses and/or agricultural species (e.g. for tropical species: *Theobroma*, Gómez-Vera et al. 2021, *Coffea*, Parecido et al. 2022, *Oryza*, de Tombeur et al. 2021). Yet, to understand Si's ecological role in species-rich tropical forests, the growth and foliar nutrient responses must be compared across species. Additionally, most studies compared only two soil categories, i.e. Si-enriched versus non-manipulated soil, and thus cannot reflect responses to the wide range of plant-available Si found across tropical landscapes (Schaller et al. 2018, Ishizawa et al. 2019). To capture the strength and shape of responses (Kreyling et al. 2018) and to assess ecological consequences of variation of soil Si in tropical forests, studies of nutrient and growth responses along a gradient of plant-available Si are necessary.

Here, we comparatively assessed growth and foliar chemistry in seedlings of 12 tropical tree species along an experimental soil Si gradient, mirroring the wide range of plant-available Si of lowland tropical forests in central Panama. We tested the following hypotheses: 1) responses in foliar Si concentrations to plant-available soil Si vary across species, with stronger responses in species with higher Si uptake capacity, 2) increased plant-available soil Si should increase plant-available soil P, foliar P concentrations and growth, if plant-available soil Si displaces P from soil binding sites and thereby improves P provisioning. Species associated to P-rich soils should show stronger responses than those associated to P-poor soils, 3) if foliar Si substitutes foliar C, increased plant-available soil Si should decrease foliar C concentrations, with more negative responses in species showing strong foliar Si responses, and 4) furthermore, increased plant-available soil Si should lead to changes in foliar nutrient stoichiometry, reducing foliar N:P, C:N and C:P ratios in species experiencing Si-induced improvements in P nutrition and/or substitution of foliar C.

Material and methods

Study site and overview

We conducted a Si fertilization experiment with potted seedlings of 12 tree species in Gamboa, Panama (09°07'N, 79°42'W), which has a moist tropical climate with a mean annual temperature of 27°C and a mean annual rainfall of 2100 mm (Slot and Winter 2017). To assess the strength and shape of plant responses to plant-available soil Si and to compare them across species, we used a non-replicated gradient

design (Kreyling et al. 2018), with one individual per species randomly assigned to each of 14 soil Si levels, i.e. 14 plants per species and 168 plants in total.

Study species and plant material

We studied species from moist tropical forests in central Panama (Supporting information). Species were selected based on the following criteria: 1) a wide range of foliar Si concentrations (based on leaf collections of plants within a 50 ha forest plot in the area, K. Kitajima et al. unpubl.) suggesting different physiological Si uptake capacities, 2) a wide range of habitat associations to plant-available P (based on species occurrence records along a regional gradient of plant-available soil P; Condit et al. 2013), 3) shade-tolerant species (Rüger et al. 2009), which contribute the largest proportion of species in the area, and 4) availability of seeds before the onset of the experiment. The focal species were in 10 different plant families. In the following we refer to the species by their genus name.

Seeds were collected in forests of the Panama Canal area in October and November 2019 from at least three individual trees per species with a minimum distance of 100 m between them. Seeds were germinated and raised until cotyledon stage or development of first foliage leaves in trays on a substrate consisting of 50% local forest soil and 50% washed river sand.

Seedlings were then transplanted into individual pots (diameter: 6.5 cm, depth: 36 cm) with the experimental substrates. For each species, we selected individuals of similar size (height and number of leaves) to reduce variation in the initial biomass across individuals. Species were transplanted in two batches which grew for ca 7.5 and 10 months in the experimental substrates, respectively. Species batches explained only negligible variation when included as random factor in the statistical models and were therefore not distinguished in further analyses.

Experiment

To manipulate plant-available Si of the base substrate we added hydrophilic pyrogenic silicon dioxide (Aerosil 300, Evonik Industries AG). Aerosil 300 closely resembles the chemical and physical properties of biogenic amorphous Si (Schaller et al. 2020a) and supplementing soils with Aerosil has been shown to increase plant-available Si (Klotz et al. 2021) without changing soil pH (J. Schaller unpubl.). The base substrate was a 1:1 mixture of sieved local forest soil with very low plant-available Si and P (Cerro Pelado, selected based on Schaller et al. 2018 and Condit et al. 2013) and thoroughly washed river sand. To create the 14 experimental substrates we added Aerosil 300 in amounts ranging regularly between 0 and 45 g l⁻¹ to the base substrate. The local soil, washed river sand and amorphous Si were thoroughly homogenized using a cement mixer. Addition of Aerosil 300 led to a linear increase of plant-available Si concentrations, ranging from 5.23 to 26.54 mg kg⁻¹ in the 14

experimental substrates and covered about 85% of the natural variation of plant-available Si found in forest soils in the region (2.25–39.88 mg kg⁻¹; Schaller et al. 2018). Adding the sand to the forest soil reduced plant-available P concentrations to 0.47 mg kg⁻¹. To ensure survival of species associated to P-rich soils, we fertilized each plant using 20 ml of a half strength Hoagland solution three times within the first three months of the experiment. Throughout the experiment, plants were regularly watered and kept under intermediate light conditions (ca 10% full sunlight) and protected from rainfall. The position of species and treatments was randomized.

We sampled each of the 14 thoroughly mixed experimental substrates (one sample per Si level) before the experiment to analyse the maximum plant-available Si concentration the plants were exposed to. To ensure the detection of interactions between plant-available Si and P in the soil, we additionally analysed plant-available P in the experimental substrates (without fertilization or plants) at the end of the experiment.

At the end of the experiment, leaves and stems of each individual were harvested, cleaned to remove any potential residual soil material, oven-dried for 48 h at 65°C, and weighed to quantify aboveground growth. Foliar Si, C, N and P concentrations were analysed, and foliar stoichiometric ratios calculated. Total foliar nutrient contents were calculated multiplying the respective foliar concentration by foliar biomass.

Chemical analysis of soils and leaves

Silicon and phosphorus

Samples of the experimental substrates were air-dried, crushed to break up large aggregates, and sieved to remove roots and stones. Plant-available Si was extracted in CaCl₂ following Schaller et al. (2018). Three g of sifted soil were shaken with 30 ml of 0.01 M CaCl₂ for 1 h at ambient laboratory temperature. The suspension was centrifuged (8000×g, for 10 min) and the supernatant decanted.

Plant-available P was extracted following the Mehlich-III method (Sims 1989). Five g of sifted soil was extracted using 10 ml g⁻¹ Mehlich III solution (0.015 M NH₄F, 0.001 M EDTA, 0.25 M NH₄NO₃, 0.00325 M HNO₃, 0.2 M HAc). Samples were shaken for 5 min at 200 min⁻¹ and centrifuged for 5 min at 10 000×g. Afterwards, the supernatant was filtered using a 0.2 µm cellulose acetate filter.

Leaves were ground for chemical analyses. Foliar Si was extracted for five h by an alkaline method using 30 mg of leaf material and 30 ml of 0.1 M sodium carbonate solution (Na₂CO₃) in a regularly shaken water bath at 85°C (Katz et al. 2021). The solution was centrifuged (3000×g, for 5 min) and passed through a 0.45 µm cellulose acetate filter (Rausch 2021). Foliar P was extracted by digesting the leaf material with HNO₃ and H₂O₂ in a closed vessel microwave digestions system (Mars express6, CEM, Germany).

The Si and P concentration of the leaf and soil extracts was determined with inductively coupled plasma optical-emission spectrometry (ICP-OES) using an elemental analyser.

Carbon and nitrogen

Foliar C and N concentrations were analysed with EA-IRMS coupling (Elemental Analyzer NA 1108, CE Instruments; Interface ConFlo III, Finnigan MAT; isotope ratio mass spectrometer: delta S, Finnigan MAT) and calculated from samples weights and peak areas as detailed by Liebel et al. (2010).

Statistical analysis

Data of individuals that did not survive the experiment or produced extremely low aboveground biomass (individuals below the 5% percentile for aboveground biomass) were removed before analyses. We calculated pairwise Spearman rank correlations among all parameters (foliar nutrient concentrations, total nutrient contents and stoichiometry, and foliar and total aboveground growth) across all species to check for collinearity (Supporting information). We excluded foliar growth and total nutrient contents from further analyses due to their high positive correlation with total aboveground growth ($r > 0.8$), and excluded Si:C ratios based on their strong correlation with foliar Si concentrations ($r = 0.99$).

To assess effects of increasing plant-available Si (treatment) on foliar Si and aboveground growth as well as on foliar P, C, and N concentrations and their stoichiometry (N:P, C:N and C:P), we used linear mixed-effects models including species as random effect ($n = 151$). To evaluate whether the effects of plant-available Si on growth and foliar nutrient status varied across species, we ran ANCOVAs and tested for species × treatment interactions ($n = 151$). Furthermore, to assess the direction and strength of each species' response in each parameter, we ran separate ordinary linear models to get the respective slope estimate (β , $n = 11–13$). We determined the species' capacities to take up Si from the linear models for foliar Si, using their fitted foliar Si concentration at maximum plant-available Si. We used a threshold value of 5 mg g⁻¹ to separate species with low and high Si uptake capacities (for similar approach compare Ishizawa et al. 2019). To test if experimentally increased plant-available Si leads to higher plant-available P, we ran an ordinary linear model ($n = 14$). We applied graphical model diagnostics to ensure normality and homogeneity in residuals. If necessary, we log₁₀-transformed the respective response parameter. The % increase (or decrease) in the parameters under the highest compared to the lowest Si availability (based on fitted values) is presented in the text where appropriate.

We tested if the responses in foliar Si and C concentrations are related to the species' Si uptake capacities by correlating the slopes of the single-species models (i.e. responses in foliar Si and C) to the fitted foliar Si concentrations at maximum plant-available Si (Pearson correlation, $n = 12$). We also tested if the responses in aboveground growth and foliar P concentrations are related to the species' habitat association to plant-available P (i.e. P effect sizes from Condit et al. 2013) by correlating them with the slopes of the single-species models (i.e. responses in aboveground growth and foliar P; Pearson correlation, $n = 11$).

All statistical analyses were performed in R ver. 4.1.0 (www.r-project.org). Linear mixed-effect models were fit using the 'lmerTest' package (Kuznetsova et al. 2017).

Results

Of the 12 focal species, eight reached foliar Si concentrations considered to reflect a high physiological Si uptake capacity ($> 5 \text{ mg g}^{-1}$), while the remaining species exhibited low Si uptake capacities. Overall, increasing plant-available Si led to increased foliar Si concentrations and higher aboveground growth, and it affected foliar C and N concentrations, and nutrient stoichiometry (Table 1). All responses were linear and we did not find any indication for non-linear responses, e.g. patterns in the data or model residuals indicating saturation or hump-shaped relationships. However, effects were concentrated on four of the 12 species and were strongly species-specific.

Below, we will present for each of the analysed parameters the overall effect of plant-available Si (treatment effect in linear mixed effect model with species as random effect), whether effects differed across species (species \times treatment in ANCOVA), how many individual species responded to soil Si (linear models for single species) and how the species' responses correlate with their Si uptake capacities or habitat associations to plant-available P (Fig. 1).

Foliar Si concentrations increased significantly with plant-available Si across species (Table 1) and the direction of the species' responses was consistent (no species \times treatment interaction, Supporting information). The increase was significant in seven species (Fig. 2a, Supporting information), which displayed a 64–140% increase in foliar Si under the highest compared to the lowest Si availability. For three other species there was weak evidence (i.e. $0.05 \leq p \leq 0.10$, compare Muff et al. 2022) for an increase in foliar Si concentrations. Only two species showed no response. In line with our first hypothesis, the relationship between the species' foliar Si responses to soil Si (β in the Supporting information) and their fitted foliar Si concentration at maximum

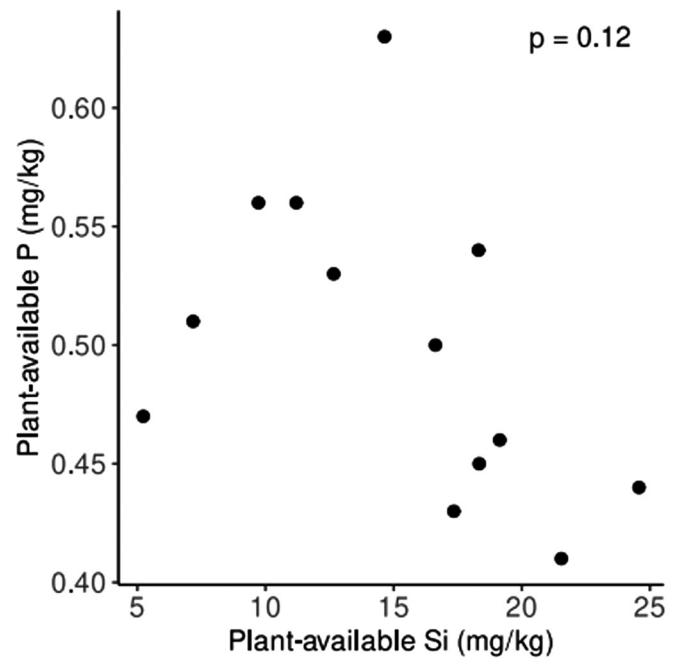


Figure 1. Relationship between plant-available P and Si concentrations along the experimental soil Si gradient ($n = 14$).

plant-available Si, reflecting their physiological uptake capacity, was positive and statistically significant (Fig. 2b).

Aboveground biomass, reflecting growth over the experimental period, increased significantly with plant-available Si across species (Table 1), and the species' responses were again consistent (no species \times treatment interaction, Supporting information). In *Herrania* and *Dendropanax* the growth increase with plant-available Si was significant (increase by 63 and 220%, respectively; Fig. 3a, Supporting information). In one species (*Theobroma*) there was weak evidence for an increase in growth along the soil Si gradient (increase by 79%). Yet, at the soil-level, increasing plant-available Si did not enhance P availability to plants ($\beta = -0.005$, $t = -1.70$, $p = 0.117$; Fig. 1), as we had hypothesized. Furthermore, no relationship emerged between the species' growth responses and their habitat association to plant-available P (Fig. 3b).

Increasing plant-available Si did not influence foliar P concentrations across species, but significantly decreased foliar N. We found weak evidence that plant-available Si decreases foliar C concentrations (Table 1). Significant, but opposite, responses in foliar P concentrations occurred in two species, with *Sorocea* showing an increase of 52% and *Theobroma* showing a 50% reduction (Fig. 4a, Supporting information). Nevertheless, no species \times treatment interaction emerged for foliar P (Supporting information). Responses in foliar C concentrations were species-specific (species \times treatment interactions, Supporting information) with four species showing a significant decrease between 4 and 13% (Fig. 4b, Supporting information), consistent with our hypothesis. Foliar N responses did not vary across species (no species \times treatment interaction, Supporting information), yet we found a significant reduction by 14 and 21% in foliar N along the

Table 1. Effects of plant-available Si on foliar Si concentration, aboveground growth (BM), foliar P, C and N concentrations and foliar N:P, C:N and C:P ratios across the 12 study species. Given are the results of linear mixed-effect models. Foliar Si, C, C:N and C:P as well as aboveground growth were \log_{10} -transformed. Significant p-values ($p \leq 0.05$) and p-values indicating weak evidence for an effect ($0.05 < p \leq 0.1$) are marked in bold and italics.

	β	SE	df	t	p
Si	0.013	0.002	139.00	6.61	<0.001
BM	0.005	0.002	139.07	2.44	0.016
P	-0.000	0.003	139.20	-0.09	0.931
C	-0.000	0.000	139.10	-1.97	<i>0.052</i>
N	-0.008	0.003	139.08	-2.43	0.017
N:P	-0.088	0.042	139.16	-2.09	0.039
C:N	0.001	0.001	139.10	1.88	<i>0.063</i>
C:P	-0.000	0.001	139.10	-0.43	0.670

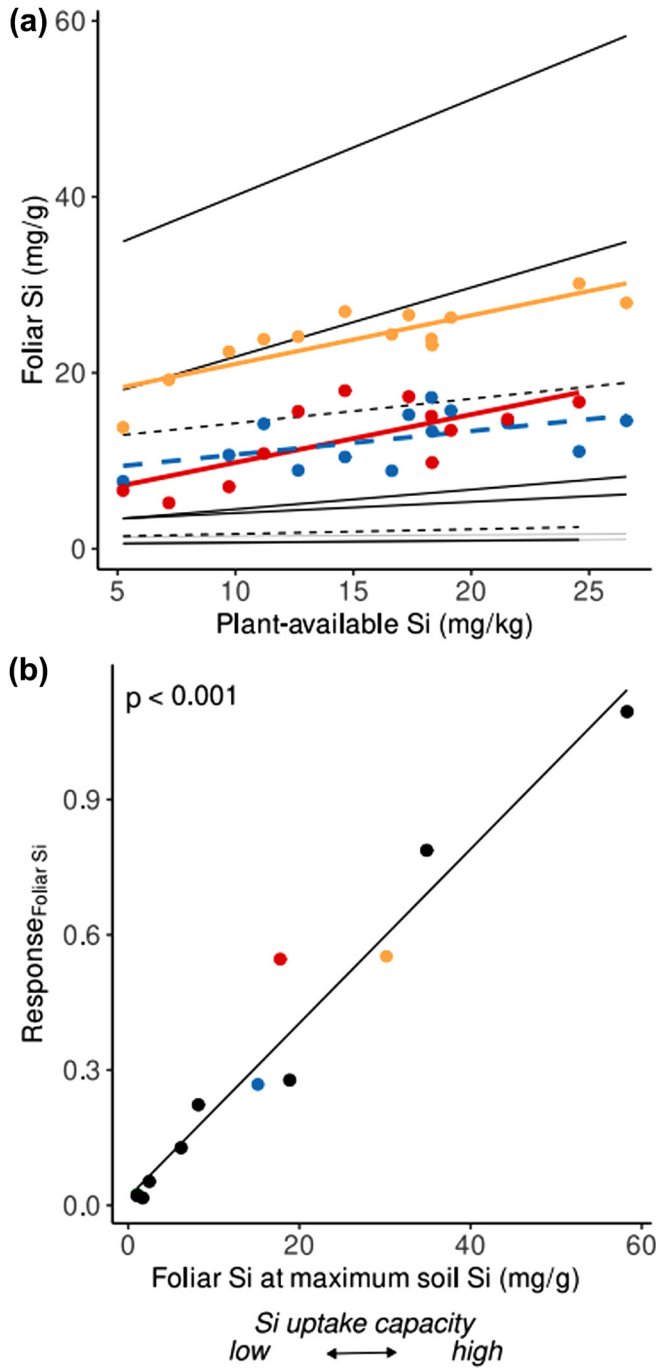


Figure 2. (a) Relationship between plant-available Si and foliar Si concentrations for 12 tropical tree species and (b) correlation ($r=0.97$) between the species' foliar Si responses to increasing plant-available Si (Response_{Foliar Si}, β of species model) and their fitted foliar Si concentrations at maximum soil Si. Black and coloured lines indicate significant relationships (solid line; $p \leq 0.05$ in (a) and $p \leq 0.001$ in (b)) and relationships with weak evidence in the data (dashed line, $0.05 < p \leq 0.1$). Grey lines indicate relationships without evidence. In (a) p-values are based on species-level ordinary linear models and in (b) on Pearson correlation. Colours indicate species highlighted in the text: *Sorocea* (yellow), *Theobroma* (red), *Dendropanax* (green) and *Herrania* (blue). In (b) the solid line represents a fitted linear regression for visualization.

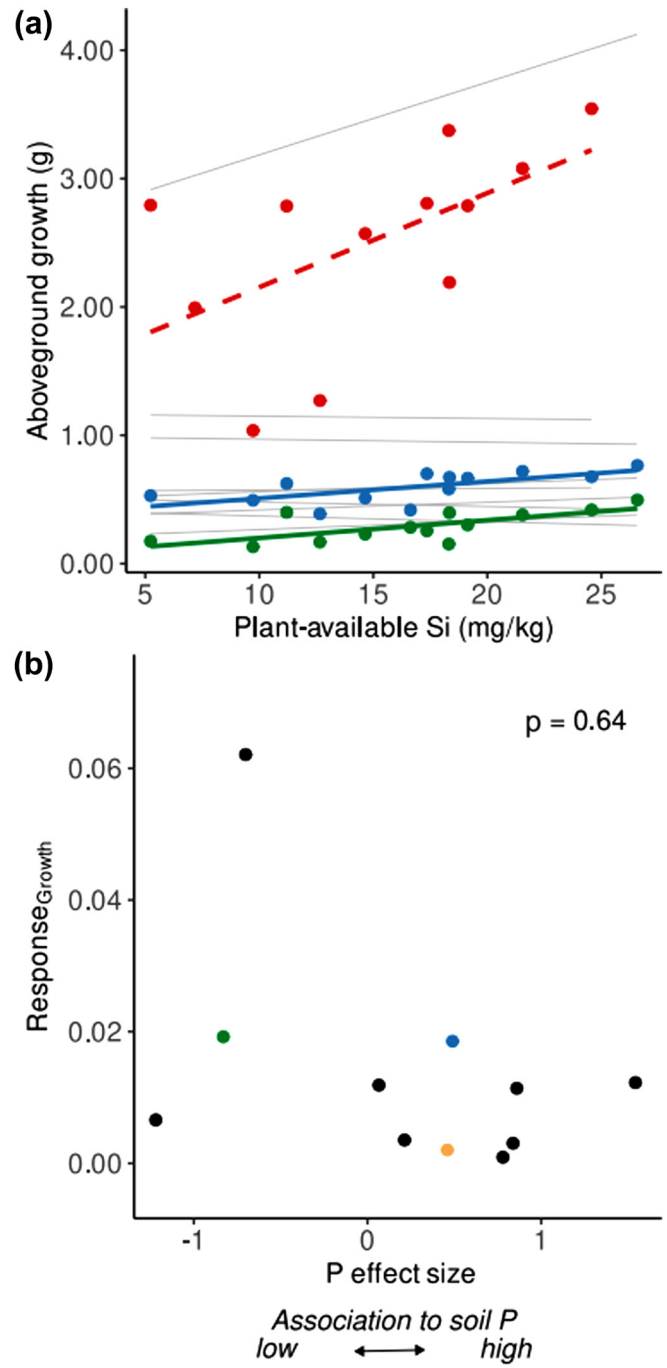


Figure 3. (a) Relationship between plant-available Si and aboveground growth for 12 tropical tree species, and (b) correlation ($r=-0.40$, $p=0.22$) between the species' aboveground growth responses to increasing plant-available Si (Response_{Growth}, β of species model) and their habitat associations to plant-available P (P effect sizes in Condit et al. 2013). In (a) coloured lines indicate significant relationships (solid line, $p \leq 0.05$) and relationships with weak evidence in the data (dashed line, $0.05 < p \leq 0.1$). Grey lines indicate relationships without evidence. In (a) p-values are based on species-level ordinary linear models and in (b) on Pearson correlation. Colours indicate species highlighted in the text: *Sorocea* (yellow), *Theobroma* (red), *Dendropanax* (green) and *Herrania* (blue).

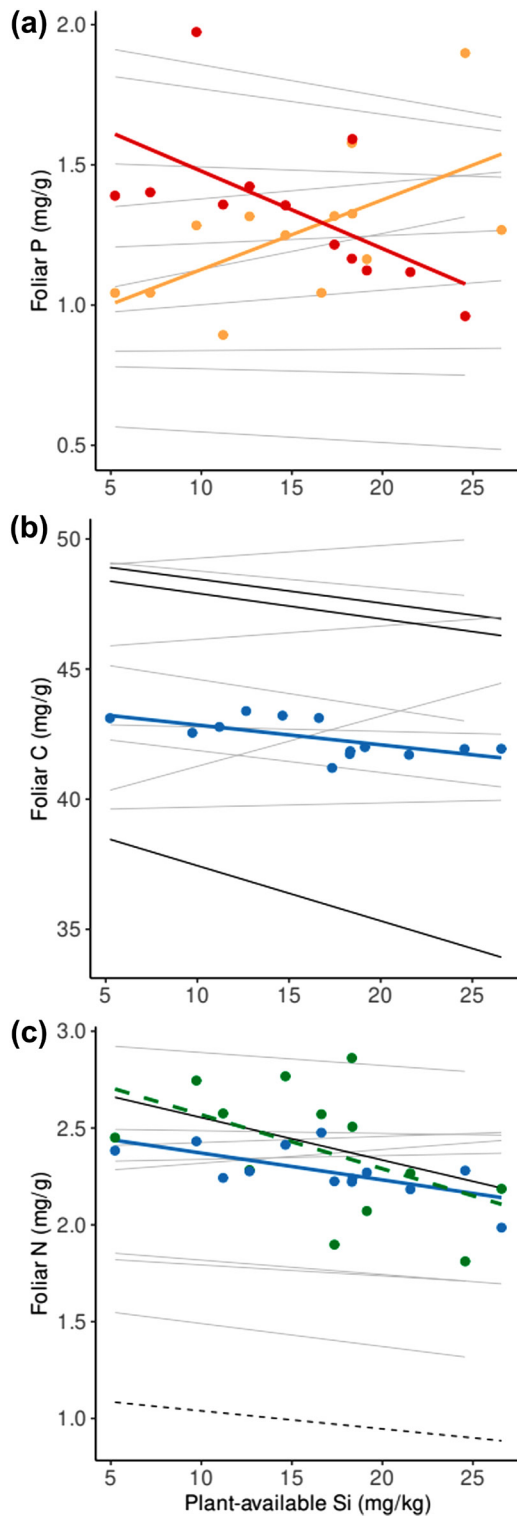


Figure 4. Relationship between plant-available Si and (a) foliar P, (b) foliar C and (c) foliar N concentrations for 12 tropical tree species. Black and coloured lines indicate significant relationships (solid line; $p \leq 0.05$) and relationships with weak evidence in the data (dashed line, $0.05 < p \leq 0.1$). Grey lines indicate relationships without evidence. p -values are based on species-level ordinary linear models. Colours indicate species highlighted in the text: *Sorocea* (yellow), *Theobroma* (red), *Dendropanax* (green) and *Herrania* (blue).

soil Si gradient in two species. In two other species, there was weak evidence for a decrease in foliar N concentrations (Fig. 4c, Supporting information). No relationship emerged between foliar P responses and the species' habitat association to plant-available P ($r = -0.16$, $p = 0.64$). The relationship between foliar C and Si responses was negative and significant ($r = -0.60$, $p = 0.04$).

As for foliar nutrient stoichiometry, foliar N:P decreased significantly and there was weak evidence for an increase in C:N ratios with plant-available Si across species (Table 1), while C:P ratios remained unaffected. The responses did not vary across species (no species \times treatment interaction, Supporting information). In *Sorocea* and *Theobroma* significant responses in foliar N:P and C:P ratios emerged, but with opposite direction. *Sorocea* displayed a 47% decrease in foliar C:P and a 39% decrease in N:P ratios (from 22 to 16) along the soil Si gradient, while in *Theobroma* foliar C:P increased by 46% and N:P by 33% (from 9 to 12; Fig. 5a, c, Supporting information). In two other species (*Herrania* and *Dendropanax*) we found weak evidence for increases in foliar C:N ratios (Fig. 5b, Supporting information).

Discussion

Increasing plant-available Si led to increased foliar Si concentrations and higher aboveground growth, and it affected foliar C and N concentrations, and nutrient stoichiometry across species. More than half of the species showed positive growth responses or changes in foliar macronutrient concentrations and/or stoichiometry along the experimental soil Si gradient. Yet, within the single parameters only a small subset of two to four species showed significant responses.

Species-specific foliar Si responses to plant-available Si

Responses in foliar Si concentrations to increasing plant-available Si were highly species-specific and stronger in species with high Si uptake capacities. Both active, transporter-driven and passive, transpiration-driven, Si uptake determine a species' capacity to take up Si (Liang et al. 2006), and their relative contributions vary substantially across species (Liang et al. 2006). Since we kept environmental factors known to influence passive Si uptake (e.g. light and water availability; Kajino and Kitajima 2021, Quigley and Anderson 2014), constant across species and along the soil Si gradient, the species-specific foliar Si responses we observed were probably driven by physiological differences in active instead of passive Si uptake. Only two species did not respond to plant-available Si and their Si uptake capacities were the lowest of all species studied. These species might lack membrane channels (aquaporins) permeable to Si and facilitating the diffusion of Si, and/or functional active Si transporters (Deshmukh and Bélanger 2016). Furthermore, in line with responses found in temperate grassland species (Klotz et al. 2021), but contrary to findings in a crop species (Faisal et al. 2012), we found no indication that species with

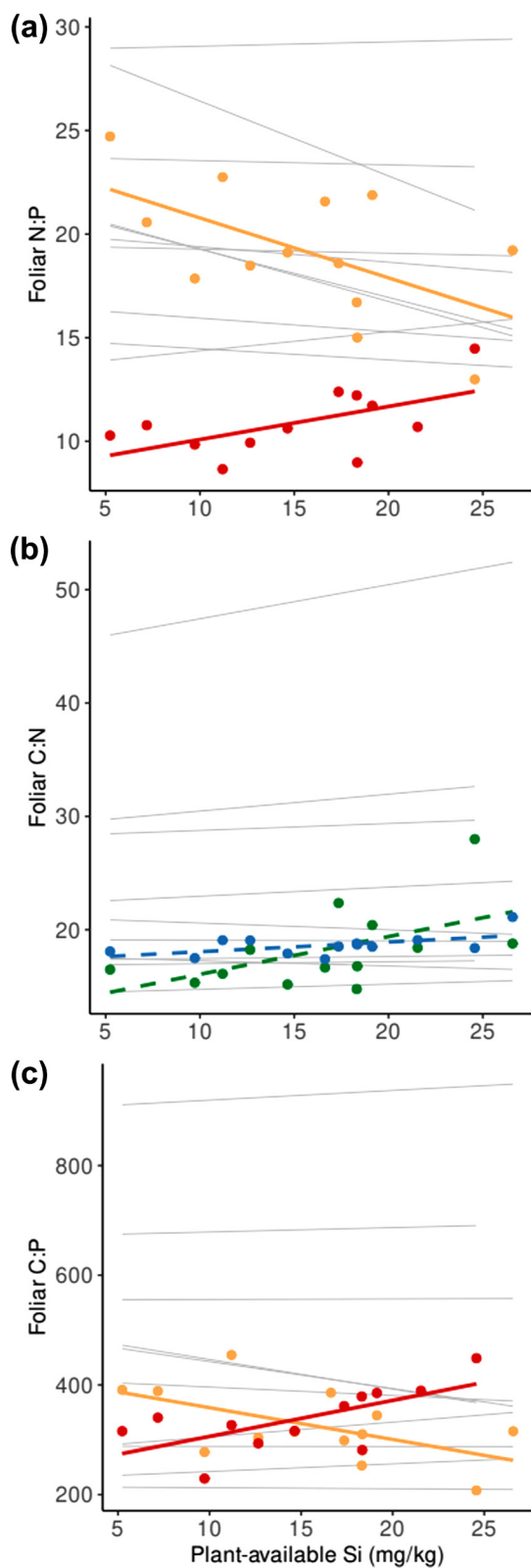


Figure 5. Relationship between plant-available Si and (a) foliar N:P, (b) C:N and (c) C:P ratios for 12 tropical tree species (for details see Fig. 4).

high Si uptake capacity upregulated Si uptake under low soil Si availability, e.g. to maintain possible performance-enhancing effects of high foliar Si concentrations. Interestingly, the Si uptake capacities determined in our study correlated with mean foliar Si concentrations measured in conspecifics on Barro Colorado Island, Panama ($r=0.71$, $p=0.02$), within a 50 ha forest plot (K. Kitajima et al. unpubl.). In line with our findings, another field study in the area showed that species with low Si uptake capacities had relatively weak and inconsistent foliar Si responses across sites differing in plant-available Si (Schaller et al. 2018). Hence, field data may provide a useful proxy for Si uptake capacities of species and their foliar Si responses to changing plant-available Si. Overall, our data suggests pronounced foliar Si responses across sites varying in plant-available Si are more likely in species with high Si uptake capacities, while species with low Si uptake capacities might not respond and/or their foliar Si responses might be overruled by other environmental factors.

Effects of Si on seedling growth of tropical tree species

Increasing plant-available Si led to overall higher above-ground growth across species. Nevertheless, at the species level, evidence of a positive (and with about 60–220% rather strong) growth response emerged only in three of the 12 species studied. Performance-enhancing effects of Si have been studied mainly in agricultural species (Cooke and Leishman 2011, 2016), which are typically fast-growing and exposed to high resource availability. In contrast, shade-tolerant tropical forest species are slow-growing and their performance is strongly limited by multiple environmental factors, including light and nutrients (Rüger et al. 2009, Vitousek et al. 2010, Wright 2019). Studies have demonstrated positive effects of Si fertilization on the growth of cultivated tropical tree species, specifically cacao *Theobroma* (Gómez-Vera et al. 2021) and coffee *Coffea* (Parecido et al. 2022). Yet, to our knowledge, we are the first to show positive growth responses to plant-available Si in tropical tree species not used for agriculture (*Herrania* and *Dendropanax*). Furthermore, these responses emerged in species with both low and high Si uptake capacities, consistent with previous work showing that a high physiological Si uptake capacity is not necessary for plants to gain beneficial effects from Si (Cooke and Leishman 2016). The effect of Si in plants might depend on whether Si is primarily bound as amorphous Si deposits which consume high amounts of mono-silicic acid or remains dissolved and thus potentially more reactive (but see Coskun et al. 2019), in which case low amounts of Si might be sufficient to cause beneficial effects. All in all, considering the vast local- and regional-scale variation in plant-available Si in tropical forests, the effects of Si on the growth of seedlings of tropical tree species might have consequences for species performance rankings across sites varying in plant-available Si.

We specifically tested whether seedling growth was improved by Si-induced increases in plant-available P. No such effect was observed, i.e. Si fertilization did not increase

plant-available P nor foliar P, and growth responses were independent of the species' habitat association to plant-available P. Our substrate was extremely P-poor and, as a result, the amount of P bound to soil minerals may have been insufficient to allow for P release through competition with dissolved mono-silicic acid – a mechanism experimentally shown in temperate and arctic soils with substantially higher total P concentrations (Schaller et al. 2019, 2020b). Whether a comparable mechanism may occur in tropical soils with higher P concentrations remains to be investigated. Since plant-available P was not increased in our study, the growth enhancements we observed must have been due to modulation of physiological mechanisms along the soil Si gradient. Many studies, including those on cacao and coffee, reported that Si increased photosynthesis (Cooke and Leishman 2016, Gómez-Vera et al. 2021) and nutrient use efficiency (Neu et al. 2017, Gómez-Vera et al. 2021, Parecido et al. 2022). We also found that higher growth was coupled with increased foliar C:N (weak evidence for *Herrania* and *Dendropanax*) or C:P ratios (*Theobroma*), suggesting improved nutrient-use efficiency with higher plant-available and/or foliar Si. However, the mechanisms of how Si may influence plant physiology and, e.g. improve nutrient-use efficiency, remains debated (Frew et al. 2018, Coskun et al. 2019).

In nine of the 12 species no evidence for performance-enhancing effects of Si emerged, which might have several reasons. Firstly, it was argued that beneficial effects of Si on plant performance can only be expected under biotic or abiotic stress (Coskun et al. 2019). In our experiment, for most species stress levels might have been too low for beneficial effects of Si to occur (we did not aim to stress plants in the first place). Secondly, active Si uptake requires energy and can be relatively costly (de Tombeur et al. 2022), so that only species taking up Si in a cost-efficient way should benefit from Si or if the benefits of Si uptake outweigh its cost (de Tombeur et al. 2022). Thirdly, the precise location and morphology of accumulated amorphous Si deposits might influence whether Si can be beneficial or not (Hartley et al. 2015).

Inconsistent and contrasting effects of Si on foliar P concentrations and stoichiometry

Most species (10 out of 12) did not show any foliar P responses to increasing plant-available Si. According to our data it seems unlikely that Si plays a significant physiological role in P uptake in most tropical tree species studied. However, foliar P concentrations, N:P and C:P ratios responded to plant-available Si in two species, *Sorocea* and *Theobroma*. In *Sorocea*, foliar P increased with plant-available Si, although plant-available P did not increase in the bulk soil, which suggests Si influenced physiological processes associated with P nutrition. Indeed, Si was shown to mobilise P from soil binding sites in the rhizosphere and in root cells through increased release of root exudates or complexation between dissolved mono-silicic acid and metals (e.g. Mn and Fe) in the roots (Kostic et al. 2017, Hu et al. 2020). The increase in foliar P led to a parallel reduction of foliar N:P ratios below

20, suggesting a change from P-limitation to N- and P co-limitation along the soil Si gradient (Güsewell 2004), yet no growth response emerged. In *Theobroma*, foliar P concentrations decreased with plant-available Si. This could be because the improved growth on a P-poor substrate can dilute foliar P concentrations (Quigley et al. 2020). Alternatively, it could be due to Si deposition in roots that can impede colonization of arbuscular mycorrhizal fungi (Johnson et al. 2022) and hence reduce mycorrhiza-mediated P uptake. Taken together, the different foliar P, N:P and C:P responses to plant-available Si in *Sorocea* and *Theobroma* indicated that Si modulated physiological processes governing P uptake and/or metabolism rather than soil-level processes and that such processes vary strongly across species.

No indication of interactions between Si and C in most species

Most species in our study (8 out of 12) lacked significant responses in foliar C showing that no or only very weak interaction (i.e. substitution or dilution) between Si accumulation and foliar C occurred. Thus, our data did not provide support that low resource environments, such as tropical forests, generally promote the substitution of C-based compounds by Si (Quigley et al. 2020), a metabolically cheap alternative to C (Raven 1983). Nevertheless, foliar C concentrations decreased with increasing plant-available Si in a third of the species studied, and more negative responses emerged in species with strong foliar Si responses, indicating that increased Si accumulation in leaves decreased foliar C concentrations. For these species, our findings are consistent with the widely suggested notion of Si-induced substitution of C-based compounds (Cooke and Leishman 2011, Quigley et al. 2020, Hodson and Guppy 2022). Alternatively, negative relationships between foliar Si and C concentrations can emerge because the high mass of foliar Si deposits can dilute macronutrient concentrations, including foliar C (Hodson and Guppy 2022). Overall, the physiological underpinnings of a Si-induced substitution of C-based compounds remain debated and their full appreciation requires study of cell-level processes (Hodson and Guppy 2022).

Ecological implications

Seedlings in the forest understory of tropical lowland forests experience high herbivory pressure and seasonal drought, and tree-fall disturbances expose seedlings to UV-stress (Krause et al. 2003, Engelbrecht et al. 2007, Eichhorn et al. 2010, Bagchi et al. 2014). Furthermore, the high activity of decomposers, including litter arthropods and microbes, is important for nutrient provisioning (Camenzind et al. 2018, Sayer et al. 2020). Considering that Si can deter herbivores (Alhousari and Greger 2018), hamper litter decomposition of litter arthropods and microbes (Schaller et al. 2014, Nakamura et al. 2021) and mitigate the detrimental effects of drought and UV-radiation (Cooke and Leishman 2016, Frew et al. 2018), species-specific responses in foliar Si to the wide variation of plant-available

Si in tropical forest soils (Schaller et al. 2018, Ishizawa et al. 2019) may differently modulate species' responses to adverse conditions and their interactions with herbivores and decomposers. Furthermore, indirect effects of plant-available Si on ecological processes may occur through shifts in foliar C:N and C:P ratios, which govern rates of herbivory (Coley et al. 2006, Poorter et al. 2004) and litter decomposition (Laird-Hopkins et al. 2017, Camenzind et al. 2018). This suggests that complex synergistic and/or antagonistic effects of foliar Si, C:N and C:P ratios on plant performance might be possible across species and sites, with implications for species distribution and ecosystem processes.

Acknowledgements – We thank Blexein Contreras, Felicito Chiru, Hubert Herz, Amanda Savage, Yacksecary Lopez and Anita Weissflog for supporting the setup, maintenance and harvest of the experiment, which enabled us to carry out the study throughout a lock-down due to the COVID-19 pandemic. The Smithsonian Tropical Research Inst. (STRI) and its dedicated staff provided logistical support, and we acknowledge research and collection permits from MiAmbiente. Chemical analyses were conducted at the STRI Biogeochemistry Laboratory, the BayCEER Laboratories of Analytical Chemistry and of Isotope Biogeochemistry at the Univ. of Bayreuth, and the Central Laboratory at Leibniz Centre for Agricultural Landscape Research. We also thank Kaoru Kitajima, Jared Westbrook and Joseph Wright for providing unpublished leaf Si data from the 50 ha plot on Barro Colorado Island. Open Access funding enabled and organized by Projekt DEAL.

Funding – The study was funded by the German research foundation (grants EN 699/5-1 and SCHA 1822/15-1).

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Marius Klotz: Conceptualization (supporting); Formal analysis (lead); Investigation (lead); Methodology (equal); Project administration (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Jörg Schaller:** Conceptualization (equal); Formal analysis (supporting); Funding acquisition (equal); Investigation (supporting); Methodology (equal); Project administration (equal); Supervision (equal); Visualization-Supporting; Writing – review and editing (equal). **Bettina M. J. Engelbrecht:** Conceptualization (equal); Formal analysis (supporting); Funding acquisition (equal); Investigation (supporting); Methodology (equal); Project administration (equal); Supervision (equal); Visualization (supporting); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/doi:10.5061/dryad.80gb5mkvj> (Klotz et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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