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de Tombeur, F. orcid.org/0000-0002-6012-8458, Raven, J.A. orcid.org/0000-0002-2789-3297, Toussaint, A. orcid.org/0000-0002-5738-4637 et al. (8 more authors) (2023) Why do plants silicify? Trends in Ecology & Evolution, 38 (3). pp. 275-288. ISSN 0169-5347

https://doi.org/10.1016/j.tree.2022.11.002

Why do plants silicify?

Felix de Tombeur[1,2,*,@], John A. Raven[3,4,5], Aurèle Toussaint[6], Hans Lambers[2], Julia Cooke[7], Sue E. Hartley[8], Scott Johnson[9], Sylvain Coq[1], Ofir Katz[10,11], Jörg Schaller[12], Cyrille Violle[1]

[1]CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France
[2]School of Biological Sciences and Institute of Agriculture, The University of Western Australia, Perth, Australia
[3]Division of Plant Science, University of Dundee at the James Hutton Institute, Invergowrie, United Kingdom
[4]School of Biological Sciences, The University of Western Australia, Perth, Australia
[5]Climate Change Cluster, Faculty of Science, University of Technology Sydney, Ultimo, Australia
[6]Department of Botany, Institute of Ecology and Earth Sciences, University of Tartu, Tartu, Estonia
[7]School of Environment, Earth and Ecosystem Sciences, The Open University, Milton Keynes, United Kingdom
[8]Department of Animal and Plant Sciences, University of Sheffield, Sheffield, United Kingdom
[9]Hawkesbury Institute for the Environment, Western Sydney University, Penrith, Australia
[10]Dead Sea and Arava Science Center, Mt. Masada, Tamar Regional Council, Israel
[11]Eilat Campus, Ben-Gurion University of the Negev, Eilat, Israel
[12]Leibniz Centre for Agricultural Landscape Research (ZALF), Müncheberg, Germany
*Corresponding author ; felix.detombeur@cefe.cnrs.fr
@Twitter account: @felixdetombeur
ORCID numbers: Félix de Tombeur (0000-0002-6012-8458) ; John A. Raven (0000-0002-2789-3297) ; Aurèle Toussaint (0000-0002-5738-4637) ; Hans Lambers (0000-0002-4118-2272) ; Sue E. Hartley (0000-0002-5117-687X) ; Julia Cooke (0000-0002-3178-0674) ; Scott Johnson (0000-0002-8388-8345) ; Sylvain Coq (0000-0002-7887-0247) ; Jörg Schaller (0000-0003-1996-0127)

Keywords costs; ecosystem functioning; fitness; functional trait; silicification; grassland

Abstract

Despite seminal papers that stress the significance of silicon (Si) in plant biology and ecology, most studies are focused on manipulations of Si supply and mitigation of stresses. The ecological significance of Si varies with different levels of biological organisation, and remains hard to capture. We show that the costs of Si accumulation are greater than currently acknowledged, and we discuss potential links between Si and fitness components (growth, survival, reproduction), environment and ecosystem functioning. We propose that Si is more important in trait-based ecology than currently recognized. Si potentially plays a significant role in many aspects of plant ecology, but knowledge gaps prevent us from understanding its possible contribution to the success of some clades and expansion of specific biomes.

Silicon in plant ecology

Biomineralization (see Glossary) in plants has long fascinated plant physiologists and ecologists [1], and is gaining momentum in recent years through studies of silicon (Si) and **silicification** [2]. Despite seminal papers that highlight the significance of Si as a beneficial element in plant biology [3,4], many aspects of Si in plant ecology remain puzzling. Why does the variation in foliar Si concentrations comprise several orders of magnitude in terrestrial plants, ranging from virtually none to very high concentrations greatly exceeding those of macronutrients (up to 10% dry weight) ? Does silicification have adaptative value, and does it contribute, or has it contributed, to the success of clades and the expansion of specific biomes (*e.g.*, grasslands [5])? What are the costs and benefits of Si, and can trade-offs with other **functional traits** be identified?

Although the compelling questions raised above remain unanswered, our understanding of Si in plant biology has progressed significantly in recent years. **Si transporters** have been identified in several taxa and a plant's capacity to accumulate Si is thought to be both heritable and inducible, interspecific variation is well characterised, and major functions have been identified for Si in plant tissues [6–9]. In particular, when supplied to plants, Si often increases their resistance to biotic (herbivores and microbial pathogens) and abiotic stresses (metal toxicity, salt and water stress, wind and other physical forces, UV, and nutrient deficiency), augments mechanical strength of plant organs, and, as a result, promotes plant growth and crop yields [2,7,10,11]. Several mechanisms may contribute to these benefits depending on the nature of the stress [12], though a recent model has attributed most Si-related functions to the deposition of **silica** in the apoplast, through the process of silicification [2].

The well-established functions of Si have attracted interest in its role in plant ecology [7,13–15]. The role of Si as a plant defence is better understood, and Si is increasingly seen as an important functional trait that impacts plant fitness [7,13,14,16]. However, the potential for Si to enhance fitness remains speculative, as does the importance of Si in ecological functions other than defence against herbivores and pathogens. The element is still under-appreciated by many ecologists, especially when compared with macronutrients like nitrogen (N) and phosphorus (P). In fact, significant gaps in elementary knowledge on Si – such as its costs of accumulation, and potential links with **fitness components** and environment – prevent us from better understanding variation in Si concentration and discerning its significance in plant ecology. For instance, trait-based approaches have proven to be helpful to study trade-offs in ecological strategies and constraints on evolution [17–19], but Si is underrepresented in trait-based ecology.

Here, we review the significance of Si in plant ecology at different levels of organisation. We considered Si concentration in leaves (hereafter leaf [Si], in mg g-1 dry weight), because we have significantly more information for this organ. We discuss (1) leaf [Si] variation among terrestrial plant species and its inclusion into trait-based ecology, (2) adaptive values of leaf silicification, (3) Si effect on **ecosystem processes** and (4) the costs and benefits of leaf Si accumulation.

Silicification: evolution, constraints, and trade-offs

Phylogenetic approaches are useful to understand interspecific variation in leaf [Si] [8,20–22]. Poales (*e.g.*, Poaceae, Cyperaceae, Juncaceae) accumulate more Si than plants in other orders, but substantial Si accumulation has been demonstrated for other orders as well (*e.g.*, Cucurbitales, Fabales) [8,23–25]. Interestingly, there is no single stimulus or function that explains the multiple emergences of this trait [9,22]. Phylogenetic analyses show that Si transporters in all land plants evolved from a small clade of aquaporins that do not differ substantially from the known Si transporters [21]. The potential capacity to take up and accumulate Si is probably ancestral to all land plants, and fully evolved only in the clades in which all necessary Si transporters evolved, possibly under specific evolutionary pressures [9,22,26,27].

In a pioneering work conducted in the Serengeti National Park, McNaughton et al. [28] showed that plants native to the more heavily grazed grasslands accumulate more Si than plants from less heavily grazed sites. This work supported the hypothesis that silicification has adaptive value in response to increased herbivore pressure when open grasslands expanded (*e.g.*, mid-Cenozoic) [reviewed in 5]. However, silicification might also have adaptive value in habitats characterised by seasonal aridity, low atmospheric carbon dioxide concentrations, low-nutrient availability, or strong wind exposure, and the adaptive origin of silicification may not have been the defence against mammalian grazers [29–34]. In fact, paradigms that associate grassland evolution with any single environmental factor (*e.g.*, grazing) are not well supported by chronology – at least at the global scale [9,35] – and various environmental factors may have contributed to grassland evolution in various parts of the world [35], suggesting that silicification is more likely an **exaptation**, rather than an adaptation to grazing.

In addition, environmental factors, including soil properties (*e.g.*, degree of weathering, mineral composition), might also have impacted soil Si availability which might explain the evolution of silicification [36], but soil Si availability is barely considered in evolutionary studies. For instance, overgrazing enhances the expression of P-mobilising traits in the **rhizosphere** (*e.g.*, root exudates) [37], which, in turn, increase chemical weathering and soil Si mobilisation [38]. Implementing long-term experimental evolution studies would be particularly relevant for Si, to understand its adaptive value according to different environmental parameters [39].

Leverage trait-based approaches might be useful to better understand constraints on the evolution of Si accumulation in plants and potential trade-offs or linkages with other traits having similar functions. The *global spectrum of plant form and function* (GSPFF) describes a dimensional phenotypic space made of six major traits critical to growth, survival and reproduction [18]. One major axis of variation reflects a plant size gradient (height, seed mass, specific stem density), and the other balances more conservative species with high leaf mass per area (LMA) versus more acquisitive fast-growing species with high leaf N concentration [18]. The association of leaf [Si] with the plant size axis of the GSPFF (Box 1) reflects the greater Si accumulation in leaves of non-woody compared with woody species (Box 1 and Figures S1 & S2 in Supplementary Material). Leaf silicification might play, or have played, a role in physical support and plant defence mechanisms mostly for non-woody plants, and possibly at the expense of C-based compounds such as cellulose and lignin (Box 2). As discussed above, the evolutionary history of grasslands is the most widespread argument to explain the higher levels of leaf Si in non-woody species, but silicification could also represent significant constraints for taller woody species.

Another major trait-based framework is the *leaf economics spectrum* (LES), that describes a major axis of cross-species leaf physiology comprising key traits such as LMA, leaf lifespan, N and P concentrations, and photosynthetic (A_{mass}) and respiration (R_{mass}) rates [17]. The spectrum runs from fast-growing species with rapid resource acquisition to slow-growing species with conservative strategies [17]. Evaluating if and how Si aligns with the LES is challenging because leaf [Si] might be associated with fast growth and return on C investment given its role as a growth-promoting beneficial element [40], but prominent ecological theories predict more investment in anti-herbivore defences for slow-growing species [19,41]. Cooke et al. [40] showed that species with shorter leaf lifespan generally exhibit higher leaf [Si], and concluded that Si could be a metabolically cheaper alternative to C in shorter-lived leaves and that leaf Si might be associated with the fast end of the LES. Here, despite significant relationships between leaf [Si] and the LES traits (Box 1 and Figure S3), leaf [Si] seems independent of the LES overall (Box 1), at least globally and at the interspecific level. It is possible that the implementation of the LES in Si research is most promising at the intraspecific level, or at least in a phylogenetically controlled set of related species, to reduce the strong phylogenetic signal of Si accumulation [20]. We also suggest combining trait-based approaches with metabolomics (*i.e.* tens of thousands of metabolites that are the substrates and products of enzymatic reactions) in Si research which has the potential to provide a better mechanistic understanding of trade-offs and ecological strategies [42].

For non-woody species, the question remains as to how high silicification affects leaf density, which has long been postulated [4]. Species that accumulate more Si in their leaves do, indeed, have denser leaves (greater leaf dry mass content; LDMC), because of the high density of silica compared with C-based compounds (Box 1). Leaf thickness decreases with increasing silicification (Box 1), and we suggest a trade-off between thick leaves and high degree of silicification as different solutions to minimise the impact of some biotic and abiotic stresses (*e.g.*, water stress, herbivory) and improving leaf mechanical properties [43,44]. Overall, silicification seems to be a neglected driver of the LDMC of non-woody species allowing leaf mechanical protection and/or water stress avoidance, especially for species with thinner leaves, and future studies on leaf physical strength (*e.g.*, force to punch, force to tear) should integrate Si in their framework. Leaf [Si] is also positively related with leaf mass per area (LMA), albeit with a weak R^2 (Box 1). This is possibly because silicification increases LDMC but high Si-accumulating species have thinner leaves, making the relationship with LMA unclear. Overall, we argue that phylogenetic analyses must be coupled with trait-based approaches to better identify potential trade-offs and constraints on Si evolution.

Si and plant fitness: to grow or to survive?

Positive effects of silicification on plant fitness have long been postulated [13], but convincing evidence is lacking so far. The numerous stresses mitigated by Si addition to the growth medium that can stimulate plant growth [2,6,10] led to the idea that Si is a growth-promoting, beneficial nutrient overall. This is particularly true since studies have demonstrated positive effects of Si on growth of unstressed plants too [45–47], although this remains contentious [2]. However, information on the effect of Si on plant growth is based mainly on experiments in controlled conditions in which Si is manipulated in the growth medium, and there are no studies considering leaf [Si] in relation to fitness and the three fitness components, *i.e.* growth, survival, reproduction. This gap in the literature prevents associating Si with fitness (Figure 1).

Identifying links between leaf [Si] and fitness components is challenging because of antagonistic processes (Figure 1). For instance, well-established trade-offs exist between growth and survival [48], because investment in defence or resistance traits reduces resources available for growth (*i.e.* growth-defence trade-off) [19]. High leaf [Si] might be linked to higher survival rates because it mitigates biotic and abiotic stresses, but also to growth, because of its links with plant architecture, light capture, photosynthesis, and eventually competition (Figure 1 and Box 2). The absence of clear links between leaf [Si] and the LES, as discussed above, prevents us from associating silicification with growth or survival, at least at the interspecific level. Besides, although Si supply increases grain yield in crops [45,46], no links between Si and seed production are known for natural systems (Figure 1).

Towards a siliceous growth-defence trade-off in grasses? Despite the lack of information on fitness-leaf [Si] relationships (Figure 1), recent comparative studies show that higher leaf [Si] is associated with slower growth rates in grasses [49–52]. In particular, Massey et al. [50] showed that leaf [Si] is negatively correlated with relative growth rate (RGR) and N concentration among 18 grass species. Similarly, Simpson et al. [49] found that higher leaf [Si] is associated with slower RGR among eight cultivated species. Also, Thorne et al. [51] showed a strong negative correlation between RGR and leaf [Si] among 19 rice genotypes. Although few, these studies consistently suggest (1) the existence of ignored **direct costs** associated with leaf Si accumulation, (2) that silicification might be positively associated with survival, rather than growth, and (3) the existence of a Si-mediated trade-off between these two fitness components. In addition to direct costs, **ecological costs** of Si accumulation – that emerge from interactions with other organisms (*e.g.*, plant-plant or plant-herbivore interactions) [19] – have never been considered and should also be estimated in future studies.

Potential relationships between fitness and leaf [Si] could be tested through comparative studies involving species and/or genotypes with *inherently* different [Si], or by using mutants with contrasting expression of Si transporters [53,54]. Different methods for estimating fitness have been suggested, ranging from time-consuming quantitative common garden experiments to easier but less rigorous population-level monitoring [48]. The use of Si-accumulating **model species** (*e.g.*, *Brachypodium distachyon*, *Setaria viridis*) might be valuable here, although Si functions have also been reported for non-accumulating model species, such as *Arabidopsis thaliana* [55] and thus should be also studied. More generally, Si-related functions are not restricted to accumulating species [24,56], and future fitness-Si studies should embrace different plant families and orders.

In addition to its potential link with fitness, a plant's capacity to accumulate Si in leaves is assumed to be heritable, given the evidence for genetic control of transporters [8], but highly plastic in response to environment. In particular, leaf [Si] shows plasticity in response to soil water availability [57], herbivory [7,58–60], N and P limitation [31,61] and CO_2 concentrations and temperature [52,62,63]. However, the mechanisms underlying Si plasticity to environmental changes are mostly unclear, especially regarding the relative contribution of **passive** and **active Si accumulation** [58,64]. In fact, it is very likely that multiple abiotic and biotic factors thought to directly increase plant Si accumulation also affect soil Si availability, transpiration and growth rates which will, in turn, affect [Si] in plant tissues. For instance, CO_2 and temperature might affect transpiration or soil water content, which would, in turn, affect the passive mode of Si uptake [57,62,63]. Similarly, increased Si accumulation with N or P limitation might be physiologically controlled through activation of Si transporters [65], but also due to the same Si uptake but in more or less plant biomass (*i.e.* dilution/concentration effect [66,67]). We suggest that future studies on plasticity in [Si] pay specific attention to underlying mechanisms whenever possible. In particular, determining changes in stomatal conductance and other physiological parameters would help to estimate the contribution of passive versus active Si uptake, and information on total dry matter production and total Si content to understand potential dilution/concentration effects [66].

Si, environmental factors and ecosystem functioning

Response–effect trait frameworks are commonly used in trait-based ecology to clarify the mechanistic links between environmental factors, species' traits and ecosystem functioning [68]. Metrics that consider the relative abundance of species in a community, such as the community-weighted mean (CWM), are effective and widely used to scale up from species to higher organisational levels [69–71]. Assigning more importance to dominant species and their traits is useful for better capturing the responses to environmental gradients and for understanding which effects can be expected on ecosystem processes, and with what magnitude [69,72]. This approach is starting to be used for Si [23,25,73–75] but still only rarely, although it might be particularly relevant because leaf [Si] is both a response and effect trait, in that it responds to environmental gradients and has an effect on ecosystem functioning [68] (Figure 2).

Si as a response trait In natural ecosystems, leaf [Si] is significantly affected by soil Si and water availability [32,76,77], herbivory [7,78–81], wind [34], nutrient limitation [23,30], and elevation [25] (Figure 2). Although some community-level trends with environment are clear (*e.g.*, Nakamura et al. [25] with elevation, and de Tombeur et al. [23] with soil nutrients), responses of [Si] to environmental conditions are mostly studied at the intraspecific level and mainly in grasses. Therefore, more interspecific studies along environmental gradients are needed to understand how [Si] is expressed in different ecosystems and plant communities.

Another challenge of community-level studies is to take into account intraspecific variation (Figure 2) [82]. So far, studies have reported both convergence and divergence between intraspecific and community-level [Si] responses to environment [23,25]. In addition to plasticity, as discussed above, intraspecific variation can also be driven by ontogeny [83] and local adaptation [84] (Figure 2). Although few studies are available on [Si] variation with ontogeny, we know that leaf [Si] increases with leaf age because Si continually accumulates and it is not remobilised [85], and Si can be diluted/concentrated in more or less plant biomass, just like N [83]. Examples of local adaptation with determined genetic basis are not available.

Si as an effect trait First, there is evidence that leaf [Si] can play a significant role in nutrient cycling [86,87] (Figure 2). For instance, silicified trichomes can slow down leaf decomposition of tropical trees by soil meso- and macrofauna [86], and Si accumulation can affect leaf nutrient stoichiometry and concentrations of C-based defence compounds in grasses (*e.g.*, cellulose, phenols, lignin) [88,89]. Second, leaf silicification can be induced in response to increased herbivore density [80], thereby influencing herbivore growth rates, reproduction and richness in grasslands [7,75]. Changes in wild herbivore populations affect several ecosystem processes, such as nutrient cycling, C storage or primary productivity [90]. Third, the positive effect of Si fertilisation on crop productivity suggests that community-level [Si] might be linked to annual net primary productivity (ANPP). Long-term field Si fertilisation showing increased aboveground biomass of grasses provides support for this [91]. We also note that over half of the terrestrial ANPP is attributed to actively Si-accumulating vegetation (33 Gton C yr^{-1}) [92]. Finally, Si cycling in terrestrial ecosystems affects the global Si and C cycles [92–95]. On geological time scales, plant-induced weathering of silicates consumes atmospheric CO_2, thereby affecting Earth's climate [96]. On biological time scales, Si recycling by vegetation strongly impacts soil-plant Si cycling [95,97] and affects Si transfer from land to oceans, where it is used by siliceous marine **diatoms** that contribute up to half of marine ANPP [93].

Beyond a "Si-C trade-off": rethinking the energetic costs of Si

Understanding the costs and benefits of trait values is at the very foundation of plant ecology [98]. It is paramount to understand trait variation as dependent on environment, trade-offs between traits, and more generally plant ecological strategies [99]. Since Raven's paper [4], plants trading "expensive carbon (C)" for "cheap Si" has become a pervasive idea in the recent literature [23,40,61,100], assuming apparent trade-offs between Si- and C-based components (Box 2), and that accumulation of Si incurs lower energetic costs than synthesising C-based defence compounds [4]. However, the validity of this hypothesis requires work at the cell and organ levels to better understand Si roles compared with C roles [100], and more accurate quantification of the costs of Si accumulation. If Si is effective and less costly than C-based compounds, why do not all plants invest in it, rather than in C-based compounds? Clearly, identifying the costs of plant silicification is imperative to explain the wide variation with phylogeny and environment, and why trade-offs with other traits exist. Here, we aim to update the costs of Si accumulation, by separating costs that are independent of soil Si availability, such as movement from the root cytosol to the xylem, from costs that increase with decreasing soil Si availability [101] (Box 3).

The costs related to Si movement from the root symplasm are estimated to be 2 mol ATP, well below the costs of synthesis of lignin and carbohydrates (around 13 and 7 times higher for lignin and carbohydrates, respectively) (Box 3). However, this estimation is derived for *Oryza sativa* and costs can differ among species and distribution of the Si transporters Lsi1 and Lsi2 (Box 3). Morevoer, significant gaps and controversies remain in our understanding of $Si(OH)_4$ transport in plants [102,103]. For instance, the structure of the Lsi2 putative $Si(OH)_4:H^+$ antiporter is still not well-characterized [104].

The costs related to soil Si mobilisation prior to plant uptake have been ignored so far, and doing so may challenge current thinking of Si as a cheap resource [38] (Box 3). We suggest that silicification is costlier than currently acknowledged, and that this depends primarily on soil Si availability that is limiting in many soils [105] (Box 3). Better estimating these costs would require more research at the rhizosphere level, to fill the gap between Si forms that are poorly available for plants (*i.e.* poorly-reactive minerals) and Si transporters – root exudates, mycorrhizal associations, silicate-solubilising bacteria – to better estimate Si costs.

Overall, we suggest that active Si accumulation should be considered through the lens of cost-benefit analyses, incorporating soil Si availability and Si demand for plant functions (Figure III). As discussed above, Si demand might increase in stressful conditions, or more competitive environments. Therefore, for a given soil and Si availability, a lower demand for Si would decrease the benefits relative to the costs. Eventually, greater silicification for defence or leaf construction might become less advantageous than C-based compounds, and cost-benefit analyses are mandatory to go beyond a simple economic Si-C trade-off. Beyond that, potential disadvantages of Si have been postulated (*e.g.*, toxicity, high density of Si, poorer biomechanical properties compared with C-based compounds, less effective defence against some types of herbivores) to explain why Si is not universally used by plants [4,13,40,106].

We specifically provide evidence for higher leaf density associated with silicification for non-woody species (Box 1), but other potential drawbacks mentioned above are not yet understood.

Concluding remarks

Despite a tremendous increase in Si research in plant biology in recent years, many aspects of siliceous ecology remain puzzling. Here, we reviewed the significance of Si in plant ecology at different levels of organisation and raised several questions and perspectives for future research (see Outstanding questions). We show that silicification varies between and within species, with environmental variation and other functional traits, and most likely influences plant fitness, interactions with other organisms and ecosystem processes. Si quantification in plant organs has become increasingly fast and easy in the last decade [*e.g.*, 107,108], thus paving the way towards a full integration of Si at different organisational levels of terrestrial ecology. We also provide a datafile with Si concentration in leaves of about 1800 species in the online version of this article, to encourage future studies to incorporate Si in their framework. A better comprehension of Si-related ecological processes could ultimately help us to develop more sustainable and diversified agroecosystems, in which Si might have a more central role than currently appreciated [109].

Acknowledgments

This project has received funding from the European Union's Horizon 2020 research and innovation program under the Marie Skłodowska-Curie grant agreement No. 101021641 (project SiliConomic granted to FdT), from the European Research Council (ERC) Starting grant 'Ecophysiological and biophysical constraints on domestication in crop plants' (grant ERC-StG-2014-639706-CONSTRAINTS) awarded to CV, and is supported by the TRY (http://www.try-db.org) and AusTraits initiatives on plant traits (https://austraits.org/).

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Figures legends

Figure 1 – Theoretical relationships between the functions conferred to Si, fitness components, and fitness. Silicification is thought to impact fitness positively [9,13], but experimental evidence is lacking, especially because fitness components are most of the time considered separately. Both growth (and perhaps competitive ability; [67]) and resistance functions have been ascribed to Si accumulation. Si accumulation could be linked to increased survival rates but slower growth rates (red scenario), or the opposite (green scenario). As discussed here, the red scenario is more likely (thicker lines in the plot), at least for grasses. The relationship between Si concentration and reproduction might be positive, since Si addition can increase crop grain yields, but field studies on Si and seed production for non-crop species are lacking. Overall, these gaps prevent us from understanding if Si accumulation is linked to population growth rates and the success of this trait. Adapted from Laughlin et al. [48].

Figure 2 – Silicon as both a response and an effect trait. Leaf [Si] varies across environments (with wind [34], herbivory [28], soil type and properties such as N, P and Si availability [23,32], elevation [25] and precipitation [30]), but the relative contribution of intra- and interspecific variation is still unclear. Intraspecific [Si] responses to environment can be contrasted among species (species a, b and c), thereby following or not community-level trends (community-weighted mean, *i.e.* CWM) [23,25]. [Si] affects several ecosystem processes (annual net primary productivity, litter decomposition, and nutrient cycling and the global C cycle at different time scales), the magnitude of which depends on the CWM [Si], not only in leaves but also in stems, wood and roots. Intraspecific [Si] variation can be driven by phenotypic plasticity, ontogeny, and/or local adaptation. Leaf [Si] shows plasticity in response to herbivory [7,58–60], N and P limitations [31,61] and CO_2 concentration and temperature [52,62,63], but underlying mechanisms remain unclear. Potential changes of leaf [Si] with ontogeny have been largely ignored, but leaf [Si] increases with increasing leaf age, because Si continually accumulates and is not remobilised [85], and Si can be diluted/concentrated in more or less

plant biomass (*i.e.* dilution/concentration effect, [66]). Finally, local acclimation and adaptation through changes in the expression of Si transporters (*e.g.*, Lsi1, Lsi2, Lsi3, Lsi6; [110,111]) can also be postulated. This figure was created using BioRender (https://biorender.com/).

Boxes (3)

BOX 1. Si: an overlooked trait in trait-based ecology

Studying leaf [Si] in relation with other key plant ecophysiological traits is useful to elucidate constraints on evolution, and identify trade-offs and potential links with plant strategy theories (*e.g.*, the leaf economics spectrum, global spectrum of plant form and function, Grime's C-S-R strategy) [17,18]. In spite of some exceptions [73,112], Si remains poorly considered in trait-based ecology. We found that leaf [Si] is well represented in the *global spectrum of plant form and function* [18] (Figure IA, and Table S1 for PCA results; see Supplementary Material), and aligned with the first dimension of the spectrum, *i.e.* the plant size axis (plant height, stem density, and seed mass).

Cooke et al. [40] aimed to include leaf [Si] in the *leaf economics spectrum* (LES; [17]). They showed that species with shorter leaf lifespan generally exhibit higher leaf [Si], but did not identify correlations between leaf [Si] and other LES traits [40]. With more species, we found that leaf [Si] was significantly positively related with leaf [P], A_{mass} and A_{area} and significantly negatively related with leaf lifespan and LMA (Figure S3). However, leaf [Si] was independent of the LES (Figure IB), because of weak R^2 (Figure S3) compared with the LES framework [17]. A fairly good relationship with A_{mass} was identified, however ($R^2 = 0.19$; $n = 454$).

For non-woody species that have higher leaf [Si] (Figures S1 and S2), the question remains how strong silicification affects the density of leaf tissues and leaf morphological traits [4]. We found that leaf [Si] is significantly positively related with the leaf dry mass content in non-woody species, reflecting the presence of silica in plant tissues (Figure IC). The relationship coefficient increases when leaf Si is expressed on an area-basis ($R^2 = 0.18$; $n = 458$). Leaf [Si] is also negatively related with leaf thickness and positively with LMA although the relation was less clear than for LDMC.

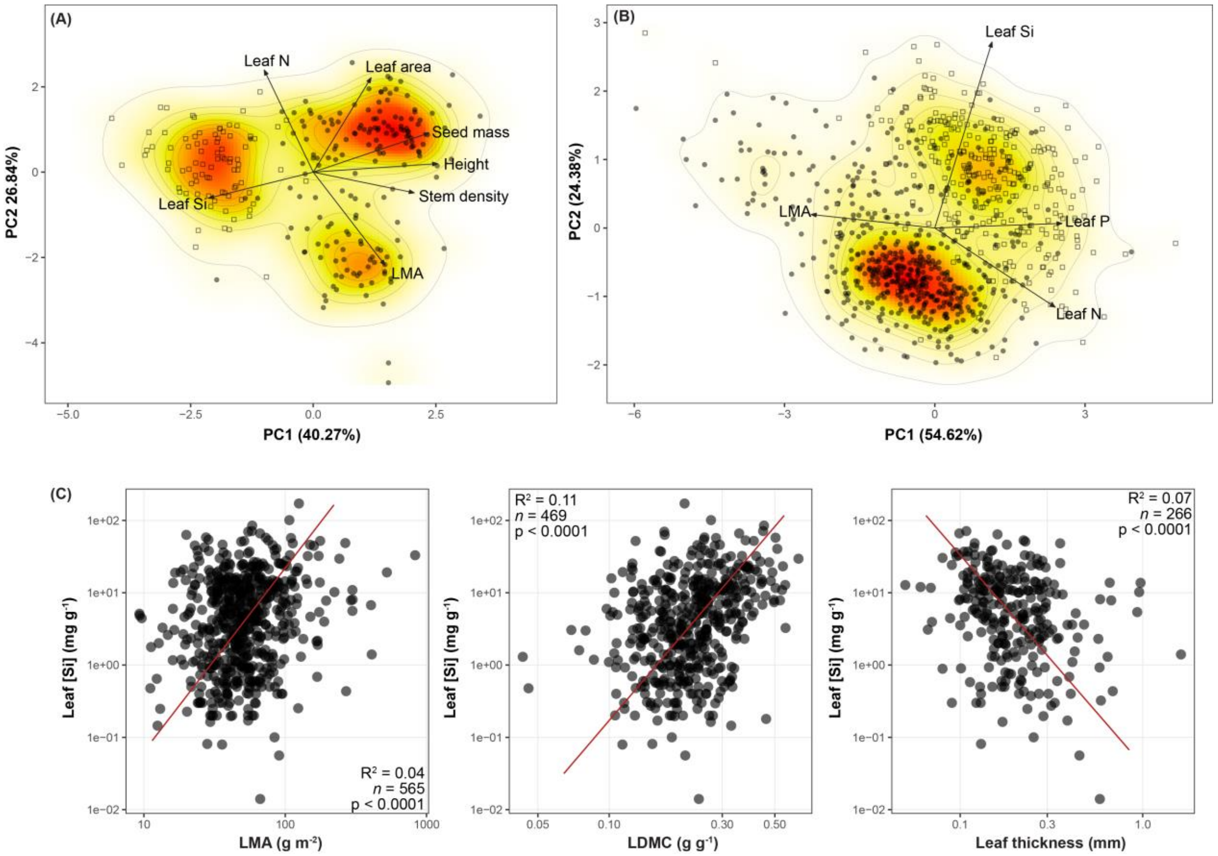

Figure I (BOX 1) - Leaf [Si] and functional trait spaces. Leaf [Si] in the *global spectrum of plant form and function* [18] with 258 species in (A), and in relation to the most-represented traits of the *leaf economics spectrum* [17] in our database (LMA, leaf N and leaf P) with 843 species in (B). In (C), bivariate relationships between leaf [Si] and LMA, leaf dry matter content (LMDC) and leaf thickness for non-woody species. These plots were obtained by compiling information on species-level leaf [Si] from 14 studies [8,15,20,21,23,25,34,74,113–118] that we crossed with two plant trait databases to extract major ecophysiological traits [119,120] (see Supplementary Material for details). In (A) and (B), the plots show the projection of species (dots) on the plane defined by the principal component (PC) axes 1 and 2. Open squares and filled circles represent non-woody and woody species, respectively. Solid arrows indicate direction and weighting of vectors representing the traits considered, and the colour gradients indicate regions of highest (red) to lowest (white) occurrence probability of species in the trait space, with contour lines indicating 0.5, 0.6, 0.7, 0.8, 0.9 and 0.99 quantiles. See also Supplementary Figures S1, S2 and S3. In (C), standardised major axis (SMA) regression lines and statistics (R²; sample size and p-values) are given for each relationship.

BOX 2. The overlooked influence of silicification on plant architecture, resistance to physical forces, and competition for light.

In grasses, Si has been linked to different plant architectural traits such as decreasing leaf insertion angle, increasing leaf straightness [44,121–123] and increasing plant height [46,67,123,124], as shown in Figure IIA. This has been attributed to the hardness of silica, which strengthens plant tissues, especially through silica deposits in cell walls [125,126]. In grasses, veins located on the abaxial epidermis made of fully silicified cells may also play a role in leaf erectness, as exemplified in sugarcane in Figure IIB [76]. Negative relationships between leaf [Si] and concentrations of C-based compounds have also been reported (*e.g.*, lignin, cellulose) which has reinforced the contention of a mechanical role of silicification, and has led to suggest "trade-offs" between Si and C components in leaves [4,44,100,127]. We found a significant negative relationship between leaf concentrations of Si and C of 838 species and driven by plant woodiness ($R^2 = 0.24$; Figure S3), suggesting that non-woody species invest relatively more in Si than in C for leaf construction/defence compounds compared with woody species. After correcting leaf [C] for silica content, the relation is weaker but still highly significant ($R^2 = 0.10$; $p < 0.0001$), suggesting that dilution is not the only factor explaining the relationship between Si and C [30]. Nevertheless, the hypothesis of a Si-C trade-off requires more work at the cell and organ levels to better understand Si roles compared with C roles [100]. Future studies on Si and C-based components should pay specific attention to mechanisms underpinning the apparent trade-off [100].

An effect of Si on plant strength may contribute to avoiding plant lodging and protection against strong winds in grasses [128], and eventually to greater photosynthetic rates due to greater light interception (Figure S3). In fact, some authors suggested that high silicification could have adaptive significance against physical forces, including wind and waves, rather than the more frequently discussed herbivore pressure [15,34]. In addition, Si-induced modifications of plant architecture may play a significant role in light capture and competition for this resource [67]. Plant height is often associated with strong competitive abilities [129], and leaf insertion angle and erectness may also affect competition for light [121]. The role of silicification on plant architecture may affect plant-plant interactions and explain the selection of this trait, but this requires further investigation [9,15,67].

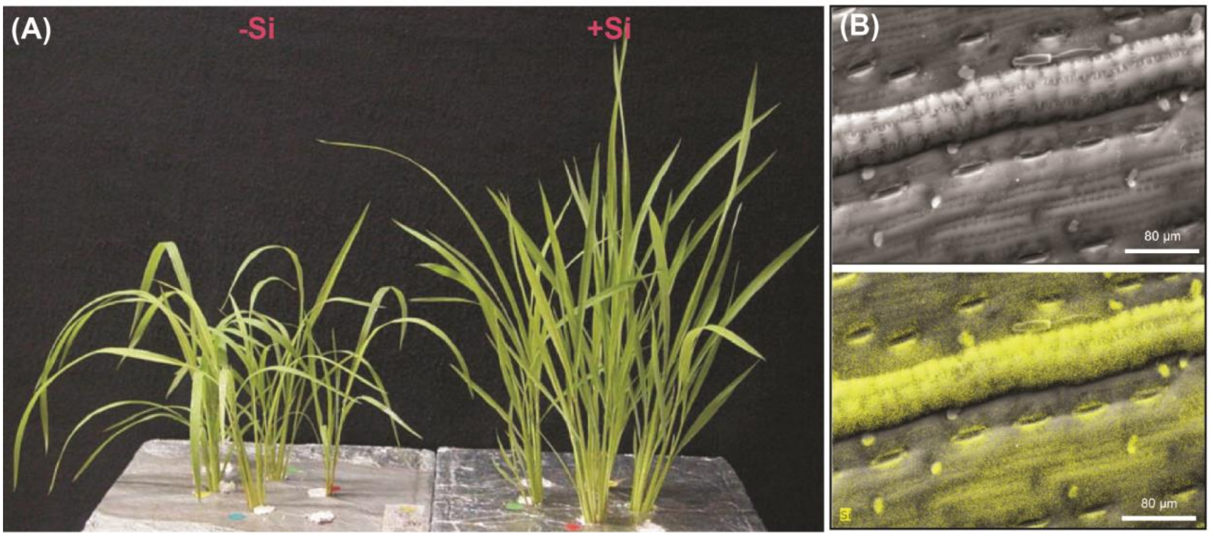

Figure II (Box 2). Influence of Si fertilisation on rice architecture modified from Zanão Júnior et al. [123] in (A), and silica deposits (white structures above, yellow signal below) on sugarcane abaxial surface leaf from de Tombeur et al. [76] in (B). Images in (B) show silica deposits along veins of about 20–70 µm wide which were formed by two to three rows of short broad epidermal cells fully silicified that could play an important role in leaf straightness.

BOX 3. The costs of silicification in plants

Costs independent of soil Si availability Transport of $Si(OH)_4$ into vascular plants has been categorised as active, passive and rejective [130]. Passive transport involves $Si(OH)_4$ uptake in the transpiration stream in the same $Si(OH)_4$:H_2O ratio as occurs in the root medium. Active uptake involves a higher, and rejective uptake a lower ratio. In *Oryza sativa*, active and passive Si-uptake co-exist, and their relative contribution depends on external $Si(OH)_4$ concentrations [130]. Active $Si(OH)_4$ uptake must occur at membrane(s) between medium and xylem sap, because $Si(OH)_4$ concentrations in xylem exudates are more than 30 times higher than concentrations in the root medium [131].

The known trans-plasmalemma proteins involved in $Si(OH)_4$ transport from the root medium to the xylem catalyse influx (Lsi1) and efflux (Lsi2). Polar location of both Lsi1 (centrifugal) and Lsi2 (centripetal) in *Oryza sativa* exodermis and endodermis suggests that the pathway of **monosilicic acid** transport from exodermis to endodermis is apoplasmic [104,132]. In some other plants, Lsi1 catalyses influx into epidermal and cortical cells, and Lsi2 catalyses efflux from endodermal cells to the xylem [104,132]. Lsi1 catalyses $Si(OH)_4$ passive influx and Lsi2 H^+ antiport efflux with a 1 mol H^+:1 mol $Si(OH))_4$ stoichiometry. With 1 mol H^+ pumped per mol ATP by the plasmalemma H^+ pump [133], 1 mol ATP is needed per mol $Si(OH)_4$ leaving a cell, so 2 mol ATP are required per mol $Si(OH)_4$ transferred from the root medium to the xylem sap of *Oryza sativa*. For plants with Lsi2 only in the endodermis, 1 mol ATP is required to move 1 mol $Si(OH)_4$ from the root medium to the xylem. Transport of $Si(OH)_4$ by Lsi1 occurs down a $Si(OH)_4$ concentration gradient from apoplasm to cytosol, with no other energisation, in agreement with the molecular structure of Lsi1 [134–136]. However, there is evidence of accumulation of $Si(OH)_4$ in the symplasm of root tips of *Oryza sativa* in both wildtype and an Lsi1 mutant [137], consistent with energised $Si(OH)_4$ transport at the plasma membrane not involving Lsi1. No evidence has been sought for the electrogenicity predicted for H^+ antiport of Lsi2 by expression in *Xenopus* oocytes. For 2 mol ATP per mol $Si(OH)_4$ moved from the root medium to the xylem, the energy cost of producing a mol of the monomers of cell wall structural compounds, lignin and polysaccharide, is 13-fold and 7-fold, respectively, of that of the inorganic substitute, SiO_2 [4]. This equivalence assumes that there is no energy cost of unloading $Si(OH)_4$ from xylem, or organic compounds associated with SiO_2 deposits, and that SiO_2 /lignin or polysaccharide monomers are structurally equivalent.

Costs dependent on soil Si availability Previous calculations [4] have assumed assumed an inexhaustible supply of $Si(OH)_4$ which is not the case in many soils worldwide [105]. Si mobilisation from poorly-available forms, and plant Si uptake are significantly increased by release of root exudates (*e.g.*, carboxylates) and arbuscular mycorrhizal associations [38,109,138]. These nutrient-acquisition strategies are costly [101], and, therefore, Si accumulation involving rhizosphere processes would be significantly more expensive than currently acknowledged [38], as is the case for P and Fe [101,139]. We argue that costs of Si accumulation would largely depend on soil Si availability (Figure III). However, whether plants increase carboxylate secretion or their association with fungi – and are therefore spending energy – in responses to Si deficiency *itself* is unknown. The possibility of changes in root morphology, mycorrhizal symbionts, and root and mycorrhizal secretions related to deficiency of Si, rather than P or some other element, deserves further investigation [38,101]. Moreover, costs of carboxylates and other Si-mobilizing root exudates may be negligible if they have already been covered by other processes (*e.g.*, to mobilise soil P) or if they result from a C surplus under conditions of growth being limited by resources other that carbon supplied in photosynthesis [140,141] (Figure III). We call for more research at the rhizosphere level to answer these compelling questions.

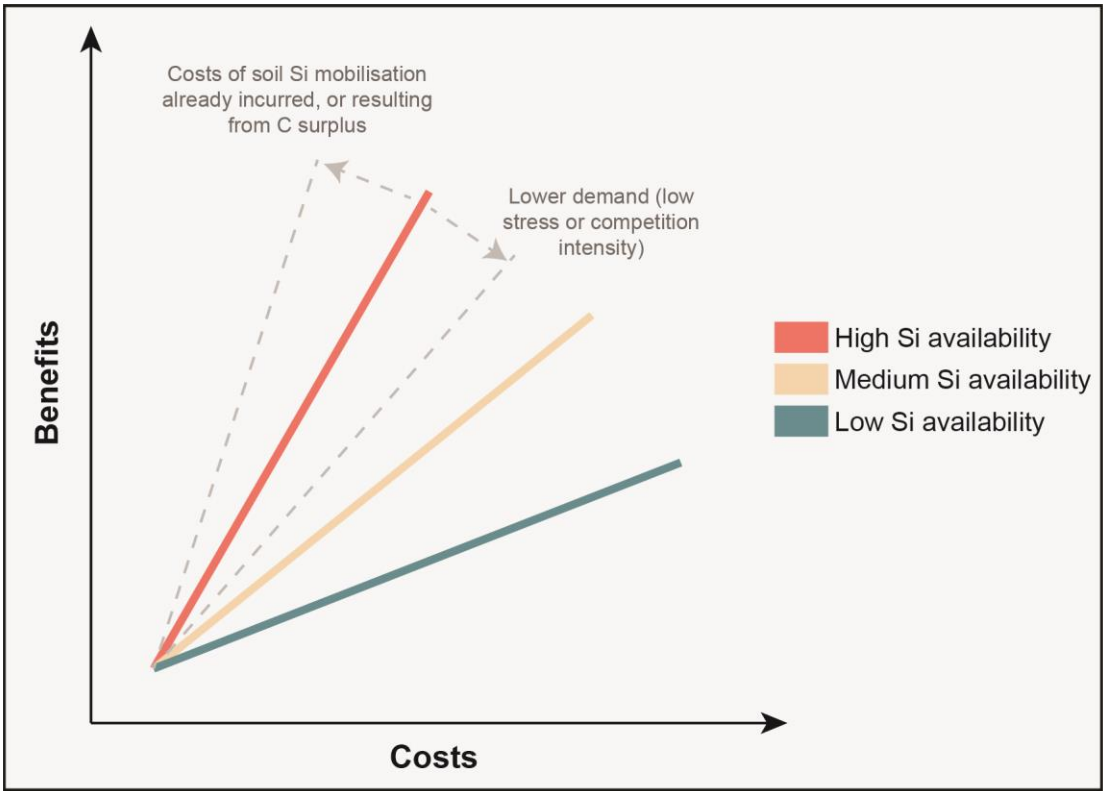

Figure III (Box 3). Schematic representation of the costs and benefits of active Si accumulation in plant organs as a function of soil Si availability. For a given soil and associated soil Si availability, a lower demand for Si, as, for instance, in less stressful and/or competitive environments, would decrease the benefits relative to the costs. Similarly, if costs of Si-mobilizing root exudates (*e.g.*, carboxylates, phytosiderophores) have already been incurred to mobilize other nutrients (*e.g.*, P or Fe) [38,101,139], or result from 'free' surplus carbon [140,141], the benefits would increase relative to the costs.

Glossary

Active Si accumulation: movement of $Si(OH)_4$ into plants from a lower to a higher $Si(OH)_4$ concentration catalysed by specific transporters energised directly (primary active transport) or indirectly (secondary active transport) by metabolism

Biomineralization: process by which organisms form minerals

Diatom: single-celled photosynthesising alga that has a silica-containing wall (frustule) and is found in almost every aquatic environment

Direct cost: a decrease in growth and/or reproduction associated with greater stress resistance (*e.g.*, growth rates, changes in phenology), not mediated by interactions with other species

Ecological cost: a decrease in growth and/or reproduction associated with greater stress resistance that manifest itself only through interactions with other organisms

Ecosystem process: a process impacting the flow of energy and matter between the biotic and abiotic components of an ecosystem; it includes primary production, trophic transfer between plants and animals, or nutrient and C cycling

Exaptation: any adaptation that performs a function different from the function that it originally held

Fitness components: individual performance including survival, growth, and reproduction; estimating fitness components yields an estimate of fitness; also called vital rates at the population level (rates of birth, death, and growth of individuals)

Functional trait: a morpho-physio-phenological trait that impacts fitness indirectly via its effects on growth, reproduction and survival

Model species: extensively studied plant species chosen for the ease of investigating particular biological phenomena

Monosilicic acid: soluble form of Si in soils, available for plant uptake, with the chemical formula $Si(OH)_4$

Passive Si accumulation: accumulation of Si in plant tissues related to transpiration driven by sunlight and related to meteorological conditions

Rhizosphere: narrow region of soil that is directly influenced by root secretions and associated soil microorganisms

Si transporter: a transplasmalemma protein catalysing $Si(OH)_4$ transport into or out of cells

Silica: silicon dioxide, with the chemical formula SiO_2. Silica in plants is amorphous and hydrated: $SiO_2.nH_2O$. It may also contain other elements, including C

Silicification: process by which an organism incorporates soluble silicic acid $Si(OH)_4$ in the form of polymerised insoluble hydrated silica ($SiO_2.nH_2O$)