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# 1 Why do plants silicify?

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## 23 Abstract

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

## 33 Silicon in plant ecology

34 **Biom mineralization** (see Glossary) in plants has long fascinated plant physiologists and  
35 ecologists [1], and is gaining momentum in recent years through studies of silicon (Si) and  
36 **silicification** [2]. Despite seminal papers that highlight the significance of Si as a beneficial  
37 element in plant biology [3,4], many aspects of Si in plant ecology remain puzzling. Why does  
38 the variation in foliar Si concentrations comprise several orders of magnitude in terrestrial  
39 plants, ranging from virtually none to very high concentrations greatly exceeding those of  
40 macronutrients (up to 10% dry weight) ? Does silicification have adaptative value, and does it  
41 contribute, or has it contributed, to the success of clades and the expansion of specific biomes

42 (*e.g.*, grasslands [5])? What are the costs and benefits of Si, and can trade-offs with other  
43 **functional traits** be identified?

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

55 The well-established functions of Si have attracted interest in its role in plant ecology [7,13–  
56 15]. The role of Si as a plant defence is better understood, and Si is increasingly seen as an  
57 important functional trait that impacts plant fitness [7,13,14,16]. However, the potential for Si  
58 to enhance fitness remains speculative, as does the importance of Si in ecological functions  
59 other than defence against herbivores and pathogens. The element is still under-appreciated by  
60 many ecologists, especially when compared with macronutrients like nitrogen (N) and  
61 phosphorus (P). In fact, significant gaps in elementary knowledge on Si – such as its costs of  
62 accumulation, and potential links with **fitness components** and environment – prevent us from  
63 better understanding variation in Si concentration and discerning its significance in plant  
64 ecology. For instance, trait-based approaches have proven to be helpful to study trade-offs in  
65 ecological strategies and constraints on evolution [17–19], but Si is underrepresented in trait-  
66 based ecology.

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

### 73 **Silicification: evolution, constraints, and trade-offs**

74 Phylogenetic approaches are useful to understand interspecific variation in leaf [Si] [8,20–22].  
75 Poales (*e.g.*, Poaceae, Cyperaceae, Juncaceae) accumulate more Si than plants in other orders,  
76 but substantial Si accumulation has been demonstrated for other orders as well (*e.g.*,  
77 Cucurbitales, Fabales) [8,23–25]. Interestingly, there is no single stimulus or function that  
78 explains the multiple emergences of this trait [9,22]. Phylogenetic analyses show that Si  
79 transporters in all land plants evolved from a small clade of aquaporins that do not differ  
80 substantially from the known Si transporters [21]. The potential capacity to take up and  
81 accumulate Si is probably ancestral to all land plants, and fully evolved only in the clades in  
82 which all necessary Si transporters evolved, possibly under specific evolutionary pressures  
83 [9,22,26,27].

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

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

103 Leverage trait-based approaches might be useful to better understand constraints on the  
104 evolution of Si accumulation in plants and potential trade-offs or linkages with other traits  
105 having similar functions. The *global spectrum of plant form and function* (GSPFF) describes a  
106 dimensional phenotypic space made of six major traits critical to growth, survival and  
107 reproduction [18]. One major axis of variation reflects a plant size gradient (height, seed mass,  
108 specific stem density), and the other balances more conservative species with high leaf mass  
109 per area (LMA) versus more acquisitive fast-growing species with high leaf N concentration  
110 [18]. The association of leaf [Si] with the plant size axis of the GSPFF (Box 1) reflects the  
111 greater Si accumulation in leaves of non-woody compared with woody species (Box 1 and  
112 Figures S1 & S2 in Supplementary Material). Leaf silicification might play, or have played, a  
113 role in physical support and plant defence mechanisms mostly for non-woody plants, and  
114 possibly at the expense of C-based compounds such as cellulose and lignin (Box 2). As  
115 discussed above, the evolutionary history of grasslands is the most widespread argument to  
116 explain the higher levels of leaf Si in non-woody species, but silicification could also represent  
117 significant constraints for taller woody species.

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

135 enzymatic reactions) in Si research which has the potential to provide a better mechanistic  
136 understanding of trade-offs and ecological strategies [42].

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

### 152 **Si and plant fitness: to grow or to survive?**

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

162 Identifying links between leaf [Si] and fitness components is challenging because of  
163 antagonistic processes (Figure 1). For instance, well-established trade-offs exist between  
164 growth and survival [48], because investment in defence or resistance traits reduces resources  
165 available for growth (*i.e.* growth-defence trade-off) [19]. High leaf [Si] might be linked to  
166 higher survival rates because it mitigates biotic and abiotic stresses, but also to growth, because

167 of its links with plant architecture, light capture, photosynthesis, and eventually competition  
168 (Figure 1 and Box 2). The absence of clear links between leaf [Si] and the LES, as discussed  
169 above, prevents us from associating silicification with growth or survival, at least at the  
170 interspecific level. Besides, although Si supply increases grain yield in crops [45,46], no links  
171 between Si and seed production are known for natural systems (Figure 1).

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

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

195 In addition to its potential link with fitness, a plant's capacity to accumulate Si in leaves is  
196 assumed to be heritable, given the evidence for genetic control of transporters [8], but highly  
197 plastic in response to environment. In particular, leaf [Si] shows plasticity in response to soil  
198 water availability [57], herbivory [7,58–60], N and P limitation [31,61] and CO<sub>2</sub> concentrations  
199 and temperature [52,62,63]. However, the mechanisms underlying Si plasticity to

200 environmental changes are mostly unclear, especially regarding the relative contribution of  
201 **passive and active Si accumulation** [58,64]. In fact, it is very likely that multiple abiotic and  
202 biotic factors thought to directly increase plant Si accumulation also affect soil Si availability,  
203 transpiration and growth rates which will, in turn, affect [Si] in plant tissues. For instance, CO<sub>2</sub>  
204 and temperature might affect transpiration or soil water content, which would, in turn, affect  
205 the passive mode of Si uptake [57,62,63]. Similarly, increased Si accumulation with N or P  
206 limitation might be physiologically controlled through activation of Si transporters [65], but  
207 also due to the same Si uptake but in more or less plant biomass (*i.e.* dilution/concentration  
208 effect [66,67]). We suggest that future studies on plasticity in [Si] pay specific attention to  
209 underlying mechanisms whenever possible. In particular, determining changes in stomatal  
210 conductance and other physiological parameters would help to estimate the contribution of  
211 passive versus active Si uptake, and information on total dry matter production and total Si  
212 content to understand potential dilution/concentration effects [66].

### 213 **Si, environmental factors and ecosystem functioning**

214 Response–effect trait frameworks are commonly used in trait-based ecology to clarify the  
215 mechanistic links between environmental factors, species’ traits and ecosystem functioning  
216 [68]. Metrics that consider the relative abundance of species in a community, such as the  
217 community-weighted mean (CWM), are effective and widely used to scale up from species to  
218 higher organisational levels [69–71]. Assigning more importance to dominant species and their  
219 traits is useful for better capturing the responses to environmental gradients and for  
220 understanding which effects can be expected on ecosystem processes, and with what magnitude  
221 [69,72]. This approach is starting to be used for Si [23,25,73–75] but still only rarely, although  
222 it might be particularly relevant because leaf [Si] is both a response and effect trait, in that it  
223 responds to environmental gradients and has an effect on ecosystem functioning [68] (Figure  
224 2).

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



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

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

### 257 **Beyond a “Si-C trade-off”: rethinking the energetic costs of Si**

258 Understanding the costs and benefits of trait values is at the very foundation of plant ecology  
259 [98]. It is paramount to understand trait variation as dependent on environment, trade-offs  
260 between traits, and more generally plant ecological strategies [99]. Since Raven’s paper [4],  
261 plants trading “expensive carbon (C)” for “cheap Si” has become a pervasive idea in the recent  
262 literature [23,40,61,100], assuming apparent trade-offs between Si- and C-based components  
263 (Box 2), and that accumulation of Si incurs lower energetic costs than synthesising C-based

264 defence compounds [4]. However, the validity of this hypothesis requires work at the cell and  
265 organ levels to better understand Si roles compared with C roles [100], and more accurate  
266 quantification of the costs of Si accumulation. If Si is effective and less costly than C-based  
267 compounds, why do not all plants invest in it, rather than in C-based compounds? Clearly,  
268 identifying the costs of plant silicification is imperative to explain the wide variation with  
269 phylogeny and environment, and why trade-offs with other traits exist. Here, we aim to update  
270 the costs of Si accumulation, by separating costs that are independent of soil Si availability,  
271 such as movement from the root cytosol to the xylem, from costs that increase with decreasing  
272 soil Si availability [101] (Box 3).

273 The costs related to Si movement from the root symplasm are estimated to be 2 mol ATP, well  
274 below the costs of synthesis of lignin and carbohydrates (around 13 and 7 times higher for lignin  
275 and carbohydrates, respectively) (Box 3). However, this estimation is derived for *Oryza sativa*  
276 and costs can differ among species and distribution of the Si transporters Lsi1 and Lsi2 (Box  
277 3). Moreover, significant gaps and controversies remain in our understanding of Si(OH)<sub>4</sub>  
278 transport in plants [102,103]. For instance, the structure of the Lsi2 putative Si(OH)<sub>4</sub>:H<sup>+</sup>  
279 antiporter is still not well-characterized [104].

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

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

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

### 299 **Concluding remarks**

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

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### 320 **References**

- 321 1 He, H. *et al.* (2014) Physiological and ecological significance of biomineralization in  
322 plants. *Trends Plant Sci.* 19, 166–174
- 323 2 Coskun, D. *et al.* (2019) The controversies of silicon’s role in plant biology. *New Phytol.*  
324 221, 67–85
- 325 3 Epstein, E. (1994) The anomaly of silicon in plant biology. *Proc. Natl. Acad. Sci. U. S.*  
326 A. 91, 11–17
- 327 4 Raven, J.A. (1983) The transport and function of silicon in plants. *Biol. Rev.* 58, 179–  
328 207
- 329 5 Strömberg, C.A.E. (2011) Evolution of grasses and grassland ecosystems. *Annu. Rev.*

- 330 *Earth Planet. Sci.* 39, 517–544
- 331 6 Debona, D. *et al.* (2017) Silicon's role in abiotic and biotic plant stresses. *Annu. Rev.*  
332 *Phytopathol.* 55, 85–107
- 333 7 Hartley, S.E. and DeGabriel, J.L. (2016) The ecology of herbivore-induced silicon  
334 defences in grasses. *Funct. Ecol.* 30, 1311–1322
- 335 8 Deshmukh, R. *et al.* (2020) New evidence defining the evolutionary path of aquaporins  
336 regulating silicon uptake in land plants. *J. Exp. Bot.* 71, 6775–6788
- 337 9 Strömberg, C.A.E. *et al.* (2016) Functions of phytoliths in vascular plants: an  
338 evolutionary perspective. *Funct. Ecol.* 30, 1286–1297
- 339 10 Cooke, J. and Leishman, M.R. (2016) Consistent alleviation of abiotic stress with silicon  
340 addition: a meta-analysis. *Funct. Ecol.* 30, 1340–1357
- 341 11 Datnoff, L.E. *et al.* (2001) *Silicon in agriculture*, Volume 8. Elsevier Science.
- 342 12 Thorne, S.J. *et al.* (2020) Is silicon a panacea for alleviating drought and salt stress in  
343 crops? *Front. Plant Sci.* 11, 1221
- 344 13 Cooke, J. and Leishman, M.R. (2011) Is plant ecology more siliceous than we realise?  
345 *Trends Plant Sci.* 16, 61–68
- 346 14 Katz, O. (2019) Silicon content is a plant functional trait: implications in a changing  
347 world. *Flora Morphol. Distrib. Funct. Ecol. Plants* 254, 88–94
- 348 15 Schoelynck, J. and Struyf, E. (2016) Silicon in aquatic vegetation. *Funct. Ecol.* 30, 1323–  
349 1330
- 350 16 Massey, F. and Hartley, S. (2009) Physical defences wear you down : progressive and  
351 irreversible impacts of silica on insect herbivores. *J. Anim. Ecol.* 78, 281–291
- 352 17 Wright, I.J. *et al.* (2004) The worldwide leaf economics spectrum. *Nature* 428, 821–827
- 353 18 Díaz, S. *et al.* (2016) The global spectrum of plant form and function. *Nature* 529, 167–  
354 171
- 355 19 Züst, T. and Agrawal, A.A. (2017) Trade-offs between plant growth and defense against  
356 insect herbivory: An emerging mechanistic synthesis. *Annu. Rev. Plant Biol.* 68, 513–  
357 534
- 358 20 Hodson, M.J. *et al.* (2005) Phylogenetic variation in the silicon composition of plants.  
359 *Ann. Bot.* 96, 1027–1046
- 360 21 Trembath-Reichert, E. *et al.* (2015) Four hundred million years of silica  
361 biomineralization in land plants. *Proc. Natl. Acad. Sci. U. S. A.* 112, 5449–5454
- 362 22 Thummel, R. V. *et al.* (2019) Evolution of phytolith deposition in modern bryophytes,  
363 and implications for the fossil record and influence on silica cycle in early land plant  
364 evolution. *New Phytol.* 221, 2273–2285
- 365 23 de Tombeur, F. *et al.* (2021) A shift from phenol to silica-based leaf defences during  
366 long-term soil and ecosystem development. *Ecol. Lett.* 24, 984–995
- 367 24 Putra, R. *et al.* (2020) Is it time to include legumes in plant silicon research? *Funct. Ecol.*  
368 34, 1142–1157

- 369 25 Nakamura, R. *et al.* (2019) Silicon cycled by tropical forest trees: effects of species,  
370 elevation and parent material on Mount Kinabalu, Malaysia. *Plant Soil* 443, 155–166
- 371 26 Katz, O. (2015) Silica phytoliths in angiosperms: Phylogeny and early evolutionary  
372 history. *New Phytol.* 208, 642–646
- 373 27 Katz, O. (2019) Conflict and complementarity of paleontological and molecular  
374 chronologies? *Paleobiology* 45, 7–20
- 375 28 McNaughton, S.J. *et al.* (1985) Silica as a defense against herbivory and a growth  
376 promotor in African grasses. *Ecology* 66, 528–535
- 377 29 Cid, M.S. *et al.* (1989) Patterns in grass silicification: response to grazing history and  
378 defoliation. *Oecologia* 80, 268–271
- 379 30 Quigley, K.M. *et al.* (2020) Soil nutrients and precipitation are major drivers of global  
380 patterns of grass leaf silicification. *Ecology* 101, e03006
- 381 31 Johnson, S.N. *et al.* (2021) Siliceous and non-nutritious: Nitrogen limitation increases  
382 anti-herbivore silicon defences in a model grass. *J. Ecol.* 109, 3767–3778
- 383 32 Quigley, K.M. *et al.* (2017) Variation in the soil ‘silicon landscape’ explains plant silica  
384 accumulation across environmental gradients in Serengeti. *Plant Soil* 410, 217–229
- 385 33 Brightly, W.H. *et al.* (2020) High silicon concentrations in grasses are linked to  
386 environmental conditions and not associated with C4 photosynthesis. *Glob. Chang. Biol.*  
387 26, 7128–7143
- 388 34 Song, Y. Bin *et al.* (2020) Association of leaf silicon content with chronic wind exposure  
389 across and within herbaceous plant species. *Glob. Ecol. Biogeogr.* 29, 711–721
- 390 35 Edwards, E.J. *et al.* (2010) The origins of C4 Grasslands: Integrating evolutionary and  
391 ecosystem science. *Science* (80-. ). 328, 587–591
- 392 36 de Tombeur, F. *et al.* (2020) Silicon dynamics during 2 million years of soil development  
393 in a coastal dune chronosequence under a Mediterranean climate. *Ecosystems* 23, 1614–  
394 1630
- 395 37 Yu, R.P. *et al.* (2020) Linking shifts in species composition induced by grazing with root  
396 traits for phosphorus acquisition in a typical steppe in Inner Mongolia. *Sci. Total*  
397 *Environ.* 712, 136495
- 398 38 de Tombeur, F. *et al.* (2021) Silicon mobilisation by root-released carboxylates. *Trends*  
399 *Plant Sci.* 26, 1116–1125
- 400 39 Kawecki, T.J. *et al.* (2012) Experimental evolution. *Trends Ecol. Evol.* 27, 547–560
- 401 40 Cooke, J. and Leishman, M.R. (2011) Silicon concentration and leaf longevity: Is silicon  
402 a player in the leaf dry mass spectrum? *Funct. Ecol.* 25, 1181–1188
- 403 41 Coley, P.D. *et al.* (1985) Resource availability and plant antiherbivore defense. *Science*  
404 (80-. ). 230, 895–899
- 405 42 Walker, T.W.N. *et al.* (2022) Functional Traits 2.0: The power of the metabolome for  
406 ecology. *J. Ecol.* 110, 4–20
- 407 43 Onoda, Y. *et al.* (2011) Global patterns of leaf mechanical properties. *Ecol. Lett.* 14,  
408 301–312

- 409 44 de Tombeur, F. *et al.* (2021) Biochar affects silicification patterns and physical traits of  
410 rice leaves cultivated in a desilicated soil (Ferric Lixisol). *Plant Soil* 460, 375–390
- 411 45 Lavinsky, A.O. *et al.* (2016) Silicon improves rice grain yield and photosynthesis  
412 specifically when supplied during the reproductive growth stage. *J. Plant Physiol.* 206,  
413 125–132
- 414 46 Ma, J. *et al.* (1989) Effect of silicon on the growth of rice plant at different growth stages.  
415 *Soil Sci. Plant Nutr.* 35, 347–356
- 416 47 Frew, A. *et al.* (2018) The role of silicon in plant biology: a paradigm shift in research  
417 approach. *Ann. Bot.* 121, 1265–1273
- 418 48 Laughlin, D.C. *et al.* (2020) The Net Effect of Functional Traits on Fitness. *Trends Ecol.*  
419 *Evol.* 35, 1037–1047
- 420 49 Simpson, K.J. *et al.* (2017) Still armed after domestication? Impacts of domestication  
421 and agronomic selection on silicon defences in cereals. *Funct. Ecol.* 31, 2108–2117
- 422 50 Massey, F.P. *et al.* (2007) Grasses and the resource availability hypothesis: The  
423 importance of silica-based defences. *J. Ecol.* 95, 414–424
- 424 51 Thorne, S.J. *et al.* (2022) The Ability of Silicon Fertilisation to Alleviate Salinity Stress  
425 in Rice is Critically Dependent on Cultivar. *Rice* 15, 8
- 426 52 Johnson, S.N. and Hartley, S.E. (2018) Elevated carbon dioxide and warming impact  
427 silicon and phenolic-based defences differently in native and exotic grasses. *Glob.*  
428 *Chang. Biol.* 24, 3886–3896
- 429 53 Tamai, K. and Ma, J.F. (2008) Reexamination of silicon effects on rice growth and  
430 production under field conditions using a low silicon mutant. *Plant Soil* 307, 21–27
- 431 54 Nakata, Y. *et al.* (2008) Rice blast disease and susceptibility to pests in a silicon uptake-  
432 deficient mutant *lsi1* of rice. *Crop Prot.* 27, 865–868
- 433 55 Fauteux, F. *et al.* (2006) The protective role of Si in the *Arabidopsis*-powdery mildew  
434 pathosystem. *Proc. Natl. Acad. Sci.* 103, 17554–17559
- 435 56 Katz, O. (2014) Beyond grasses: the potential benefits of studying silicon accumulation  
436 in non-grass species. *Front. Plant Sci.* 5, 376
- 437 57 Ryalls, J.M.W. *et al.* (2018) Silicon uptake by a pasture grass experiencing simulated  
438 grazing is greatest under elevated precipitation. *BMC Ecol.* 18, 53
- 439 58 McLarnon, E. *et al.* (2017) Evidence for active uptake and deposition of Si-based  
440 defenses in tall fescue. *Front. Plant Sci.* 8, 1199
- 441 59 Waterman, J.M. *et al.* (2020) Short-term resistance that persists: Rapidly induced silicon  
442 anti-herbivore defence affects carbon-based plant defences. *Funct. Ecol.* 35, 82–92
- 443 60 Waterman, J.M. *et al.* (2021) Short-term exposure to silicon rapidly enhances plant  
444 resistance to herbivory. *Ecology* 102, e03438
- 445 61 Minden, V. *et al.* (2021) Plants increase silicon content as a response to nitrogen or  
446 phosphorus limitation: a case study with *Holcus lanatus*. *Plant Soil* 462, 95–108
- 447 62 Biru, F.N. *et al.* (2020) Contrasting effects of Miocene and Anthropocene levels of  
448 atmospheric CO<sub>2</sub> on silicon accumulation in a model grass. *Biol. Lett.* 16, 20200608

- 449 63 Johnson, S.N. *et al.* (2019) Climate warming and plant biomechanical defences: Silicon  
450 addition contributes to herbivore suppression in a pasture grass. *Funct. Ecol.* 33, 587–  
451 596
- 452 64 Faisal, S. *et al.* (2012) Transpiration-dependent passive silica accumulation in cucumber  
453 (*Cucumis sativus*) under varying soil silicon availability. *Botany* 90, 1058–1064
- 454 65 Wu, X. *et al.* (2017) Interactions between nitrogen and silicon in rice and their effects on  
455 resistance toward the brown planthopper *Nilaparvata lugens*. *Front. Plant Sci.* 8, 28
- 456 66 Jarrell, W.M. and Beverly, R.B. (1981) The dilution effect in plant nutrition studies. *Adv.*  
457 *Agron.* 34, 197–224
- 458 67 de Tombeur, F. *et al.* (2022) Nitrogen availability and plant–plant interactions drive leaf  
459 silicon concentration in wheat genotypes. *Funct. Ecol.* In press, 10.1111/1365-  
460 2435.14170
- 461 68 Lavorel, S. and Garnier, E. (2002) Predicting changes in community composition and  
462 ecosystem functioning from plant traits: revisiting the Holy Grail. *Funct. Ecol.* 16, 545–  
463 556
- 464 69 Violle, C. *et al.* (2007) Let the concept of trait be functional! *Oikos* 116, 882–892
- 465 70 Suding, K.N. *et al.* (2008) Scaling environmental change through the community-level:  
466 A trait-based response-and-effect framework for plants. *Glob. Chang. Biol.* 14, 1125–  
467 1140
- 468 71 Garnier, E. *et al.* (2007) Assessing the effects of land-use change on plant traits,  
469 communities and ecosystem functioning in grasslands: A standardized methodology and  
470 lessons from an application to 11 European sites. *Ann. Bot.* 99, 967–985
- 471 72 Grime, J.P. (1998) Benefits of plant diversity to ecosystems: immediate, filter and  
472 founder effects. *J. Ecol.* 86, 902–910
- 473 73 Kergunteuil, A. *et al.* (2018) Plant physical and chemical defence variation along  
474 elevation gradients: a functional trait-based approach. *Oecologia* 187, 561–571
- 475 74 Schaller, J. *et al.* (2016) Plant diversity and functional groups affect Si and Ca pools in  
476 aboveground biomass of grassland systems. *Oecologia* 182, 277–286
- 477 75 Schuldt, A. *et al.* (2019) Multiple plant diversity components drive consumer  
478 communities across ecosystems. *Nat. Commun.* 10, 1460
- 479 76 de Tombeur, F. *et al.* (2020) Soil and climate affect foliar silicification patterns and  
480 silica-cellulose balance in sugarcane (*Saccharum officinarum*). *Plant Soil* 452, 529–546
- 481 77 Quigley, K.M. and Anderson, T.M. (2014) Leaf silica concentration in Serengeti grasses  
482 increases with watering but not clipping: insight from a common garden study and  
483 literature review. *Front. Plant Sci.* 5, 568
- 484 78 Huitu, O. *et al.* (2014) Silicon, endophytes and secondary metabolites as grass defenses  
485 against mammalian herbivores. *Front. Plant Sci.* 5, 478
- 486 79 Wieczorek, M. *et al.* (2015) Plant-herbivore interactions: Silicon concentration in  
487 tussock sedges and population dynamics of root voles. *Funct. Ecol.* 29, 187–194
- 488 80 Ruffino, L. *et al.* (2018) Population-level manipulations of field vole densities induce

- 489 subsequent changes in plant quality but no impacts on vole demography. *Ecol. Evol.* 8,  
490 7752–7762
- 491 81 Petit Bon, M. *et al.* (2022) Forage quality in tundra grasslands under herbivory: Silicon-  
492 based defences, nutrients and their ratios in grasses. *J. Ecol.* 110, 129–143
- 493 82 Siefert, A. *et al.* (2015) A global meta-analysis of the relative extent of intraspecific trait  
494 variation in plant communities. *Ecol. Lett.* 18, 1406–1419
- 495 83 Westoby, M. *et al.* (2022) Trait ecology of startup plants. *New Phytol.* DOI:  
496 10.1111/nph.18193
- 497 84 Albert, C.H. *et al.* (2011) When and how should intraspecific variability be considered  
498 in trait-based plant ecology? *Perspect. Plant Ecol. Evol. Syst.* 13, 217–225
- 499 85 Motomura, H. *et al.* (2002) Silica accumulation in long-lived leaves of *Sasa veitchii*  
500 (Carrière) rehder (Poaceae-Bambusoideae). *Ann. Bot.* 90, 149–152
- 501 86 Nakamura, R. *et al.* (2022) Silicious trichomes as a trait that may slow down leaf  
502 decomposition by soil meso- and macrofauna. *Plant Soil* 471, 289–299
- 503 87 Schaller, J. *et al.* (2014) Silica decouples fungal growth and litter decomposition without  
504 changing responses to climate warming and N enrichment. *Ecology* 95, 3181–3189
- 505 88 Schaller, J. *et al.* (2019) Silicon accumulation in rice plant aboveground biomass affects  
506 leaf carbon quality. *Plant Soil* 444, 399–407
- 507 89 Neu, S. *et al.* (2017) Silicon availability modifies nutrient use efficiency and content,  
508 C:N:P stoichiometry, and productivity of winter wheat (*Triticum aestivum* L.). *Sci. Rep.*  
509 7, 40829
- 510 90 Forbes, E.S. *et al.* (2019) Synthesizing the effects of large, wild herbivore exclusion on  
511 ecosystem function. *Funct. Ecol.* 33, 1597–1610
- 512 91 Xu, D. *et al.* (2020) Silicon addition improves plant productivity and soil nutrient  
513 availability without changing the grass:legume ratio response to N fertilization. *Sci. Rep.*  
514 10, 10295
- 515 92 Carey, J.C. and Fulweiler, R.W. (2012) The terrestrial silica pump. *PLoS One* 7, e52932
- 516 93 Conley, D.J. and Carey, J.C. (2015) Biogeochemistry: Silica cycling over geologic time.  
517 *Nat. Geosci.* 8, 431–432
- 518 94 Street-Perrott, F.A. and Barker, P.A. (2008) Biogenic silica: a neglected component of  
519 the coupled global continental biogeochemical cycles of carbon and silicon. *Earth Surf.*  
520 *Process. Landforms* 33, 1436–1457
- 521 95 Alexandre, A. *et al.* (1997) Plant impact on the biogeochemical cycle of silicon and  
522 related weathering processes. *Geochim. Cosmochim. Acta* 61, 677–682
- 523 96 Gaillardet, J. *et al.* (1999) Global silicate weathering and CO<sub>2</sub> consumption rates  
524 deduced from the chemistry of large rivers. *Chem. Geol.* 159, 3–30
- 525 97 de Tombeur, F. *et al.* (2020) Plants sustain the terrestrial silicon cycle during ecosystem  
526 retrogression. *Science (80-. )*. 369, 1245–1248
- 527 98 Kikuzawa, K. (1991) A cost-benefit analysis of leaf habit and leaf longevity of trees and  
528 their geographical pattern. *Am. Nat.* 138, 1250–1263



- 529 99 Westoby, M. and Wright, I.J. (2006) Land-plant ecology on the basis of functional traits.  
530 *Trends Ecol. Evol.* 21, 261–268
- 531 100 Hodson, M.J. and Guppy, C.N. (2022) Some thoughts on silicon and carbon trade-offs  
532 in plants. *Plant Soil* DOI: 10.1007/s11104-022-05394-5
- 533 101 Raven, J.A. *et al.* (2018) Costs of acquiring phosphorus by vascular land plants: patterns  
534 and implications for plant coexistence. *New Phytol.* 217, 1420–1427
- 535 102 Coskun, D. *et al.* (2019) In defence of the selective transport and role of silicon in plants.  
536 *New Phytol.* 223, 514–516
- 537 103 Exley, C. *et al.* (2020) How is silicic acid transported in plants? *Silicon* 12, 2641–2645
- 538 104 Coskun, D. *et al.* (2021) Lsi2: A black box in plant silicon transport. *Plant Soil* 466, 1–  
539 20
- 540 105 Schaller, J. *et al.* (2021) Silicon cycling in soils revisited. *Plants* 10, 295
- 541 106 Johnson, S.N. *et al.* (2021) Silicon defence in plants: does herbivore identity matter?  
542 *Trends Plant Sci.* 26, 99–101
- 543 107 Smis, A. *et al.* (2014) Determination of plant silicon content with near infrared  
544 reflectance spectroscopy. *Front. Plant Sci.* 5, 496
- 545 108 Reidinger, S. *et al.* (2012) Rapid and accurate analyses of silicon and phosphorus in  
546 plants using a portable X-ray fluorescence spectrometer. *New Phytol.* 195, 699–706
- 547 109 de Tombeur, F. *et al.* (2021) Silicon dynamics through the lens of soil-plant-animal  
548 interactions: perspectives for agricultural practices. *Plant Soil* 467, 1–28
- 549 110 Ma, J.F. and Yamaji, N. (2015) A cooperative system of silicon transport in plants.  
550 *Trends Plant Sci.* 20, 435–442
- 551 111 Huang, S. *et al.* (2022) A pericycle-localized silicon transporter for efficient xylem  
552 loading in rice. *New Phytol.* 234, 197–208
- 553 112 Descombes, P. *et al.* (2020) Plant physical and chemical traits associated with herbivory  
554 in situ and under a warming treatment. *J. Ecol.* 108, 733–749
- 555 113 Cooke, J. and Leishman, M.R. (2012) Tradeoffs between foliar silicon and carbon-based  
556 defences: Evidence from vegetation communities of contrasting soil types. *Oikos* 121,  
557 2052–2060
- 558 114 Fyllas, N.M. *et al.* (2009) Basin-wide variations in foliar properties of Amazonian forest:  
559 phylogeny, soils and climate. *Biogeosciences* 6, 2677–2708
- 560 115 Domingues, T.F. *et al.* (2010) Co-limitation of photosynthetic capacity by nitrogen and  
561 phosphorus in West Africa woodlands. *Plant, Cell Environ.* 33, 959–980
- 562 116 Adler, P.B. *et al.* (2004) Functional traits of graminoids in semi-arid steppes: A test of  
563 grazing histories. *J. Appl. Ecol.* 41, 653–663
- 564 117 Ishizawa, H. *et al.* (2019) Spatial variations of soil silicon availability and biogenic  
565 silicon flux in a lowland tropical forest in Malaysia. *Ecol. Res.* 34, 548–559
- 566 118 Klotz, M. *et al.* (2021) Variation of foliar silicon concentrations in temperate forbs:  
567 effects of soil silicon, phylogeny and habitat. *Oecologia* 196, 977–987

- 568 119 Falster, D. *et al.* (2021) AusTraits, a curated plant trait database for the Australian flora.  
569 *Sci. Data* 8, 254
- 570 120 Kattge, J. *et al.* (2020) TRY plant trait database – enhanced coverage and open access.  
571 *Glob. Chang. Biol.* 26, 119–188
- 572 121 Ando, H. *et al.* (2002) Growth and canopy structure of rice plants grown under field  
573 conditions as affected by Si application. *Soil Sci. Plant Nutr.* 48, 429–432
- 574 122 Yamamoto, T. *et al.* (2012) Effect of silicon deficiency on secondary cell wall synthesis  
575 in rice leaf. *J. Plant Res.* 125, 771–779
- 576 123 Zanão Júnior, L.A. *et al.* (2010) Rice grown in nutrient solution with doses of manganese  
577 and silicon. *Rev. Bras. Ciência do Solo* 34, 1629–1639
- 578 124 Gong, H.J. *et al.* (2003) Effects of silicon on growth of wheat under drought. *J. Plant*  
579 *Nutr.* 26, 1055–1063
- 580 125 Epstein, E. (1999) Silicon. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 50, 641–664
- 581 126 Bauer, P. *et al.* (2011) Calcium and silicon mineralization in land plants: Transport,  
582 structure and function. *Plant Sci.* 180, 746–756
- 583 127 Schoelynck, J. *et al.* (2010) Silica uptake in aquatic and wetland macrophytes: A strategic  
584 choice between silica, lignin and cellulose? *New Phytol.* 186, 385–391
- 585 128 Ma, J.F. (2004) Role of silicon in enhancing the resistance of plants to biotic and abiotic  
586 stresses. *Soil Sci. Plant Nutr.* 50, 11–18
- 587 129 Violle, C. *et al.* (2009) Competition, traits and resource depletion in plant communities.  
588 *Oecologia* 160, 747–755
- 589 130 Liang, Y. *et al.* (2006) Importance of plant species and external silicon concentration to  
590 active silicon uptake and transport. *New Phytol.* 172, 63–72
- 591 131 Mitani, N. *et al.* (2005) Identification of the silicon form in xylem sap of rice (*Oryza*  
592 *sativa* L.). *Plant Cell Physiol.* 46, 279–283
- 593 132 Mitani-Ueno, N. and Ma, J.F. (2021) Linking transport system of silicon with its  
594 accumulation in different plant species. *Soil Sci. Plant Nutr.* 67, 10–17
- 595 133 Nobel, P.S. (2005) *Physicochemical and environmental plant physiology*, 3rd  
596 Editio. Elsevier.
- 597 134 Saitoh, Y. *et al.* (2021) Structural basis for high selectivity of a rice silicon channel Lsi1.  
598 *Nat. Commun.* 12, 6236
- 599 135 van den Berg, B. *et al.* (2021) Structural basis for silicic acid uptake by higher plants. *J.*  
600 *Mol. Biol.* 433, 167226
- 601 136 Handa, N. *et al.* (2022) Aquaporin-mediated transport: Insights into metalloid  
602 trafficking. *Physiol. Plant.* 174, e13687
- 603 137 Ma, J.F. *et al.* (2004) Characterization of the silicon uptake system and molecular  
604 mapping of the silicon transporter gene in rice. *Plant Physiol.* 136, 3284–3289
- 605 138 Frew, A. *et al.* (2017) Host plant colonisation by arbuscular mycorrhizal fungi stimulates  
606 immune function whereas high root silicon concentrations diminish growth in a soil-

- 607 dwelling herbivore. *Soil Biol. Biochem.* 112, 117–126
- 608 139 Mendoza-Cózatl, D.G. *et al.* (2019) Keep talking: Crosstalk between iron and sulfur  
609 networks fine-tunes growth and development to promote survival under iron limitation.  
610 *J. Exp. Bot.* 70, 4197–4210
- 611 140 Prescott, C.E. *et al.* (2020) Surplus carbon drives allocation and plant – soil interactions.  
612 *Trends Ecol. Evol.* 35, 1110–1118
- 613 141 Prescott, C.E. (2022) Sinks for plant surplus carbon explain several ecological  
614 phenomena. *Plant Soil* 476, 689–698

615

## 616 **Figures legends**

617

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

629 **Figure 2 – Silicon as both a response and an effect trait.** Leaf [Si] varies across environments  
630 (with wind [34], herbivory [28], soil type and properties such as N, P and Si availability [23,32],  
631 elevation [25] and precipitation [30]), but the relative contribution of intra- and interspecific  
632 variation is still unclear. Intraspecific [Si] responses to environment can be contrasted among  
633 species (species a, b and c), thereby following or not community-level trends (community-  
634 weighted mean, *i.e.* CWM) [23,25]. [Si] affects several ecosystem processes (annual net  
635 primary productivity, litter decomposition, and nutrient cycling and the global C cycle at  
636 different time scales), the magnitude of which depends on the CWM [Si], not only in leaves but  
637 also in stems, wood and roots. Intraspecific [Si] variation can be driven by phenotypic plasticity,  
638 ontogeny, and/or local adaptation. Leaf [Si] shows plasticity in response to herbivory [7,58–  
639 60], N and P limitations [31,61] and CO<sub>2</sub> concentration and temperature [52,62,63], but  
640 underlying mechanisms remain unclear. Potential changes of leaf [Si] with ontogeny have been  
641 largely ignored, but leaf [Si] increases with increasing leaf age, because Si continually  
642 accumulates and is not remobilised [85], and Si can be diluted/concentrated in more or less

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

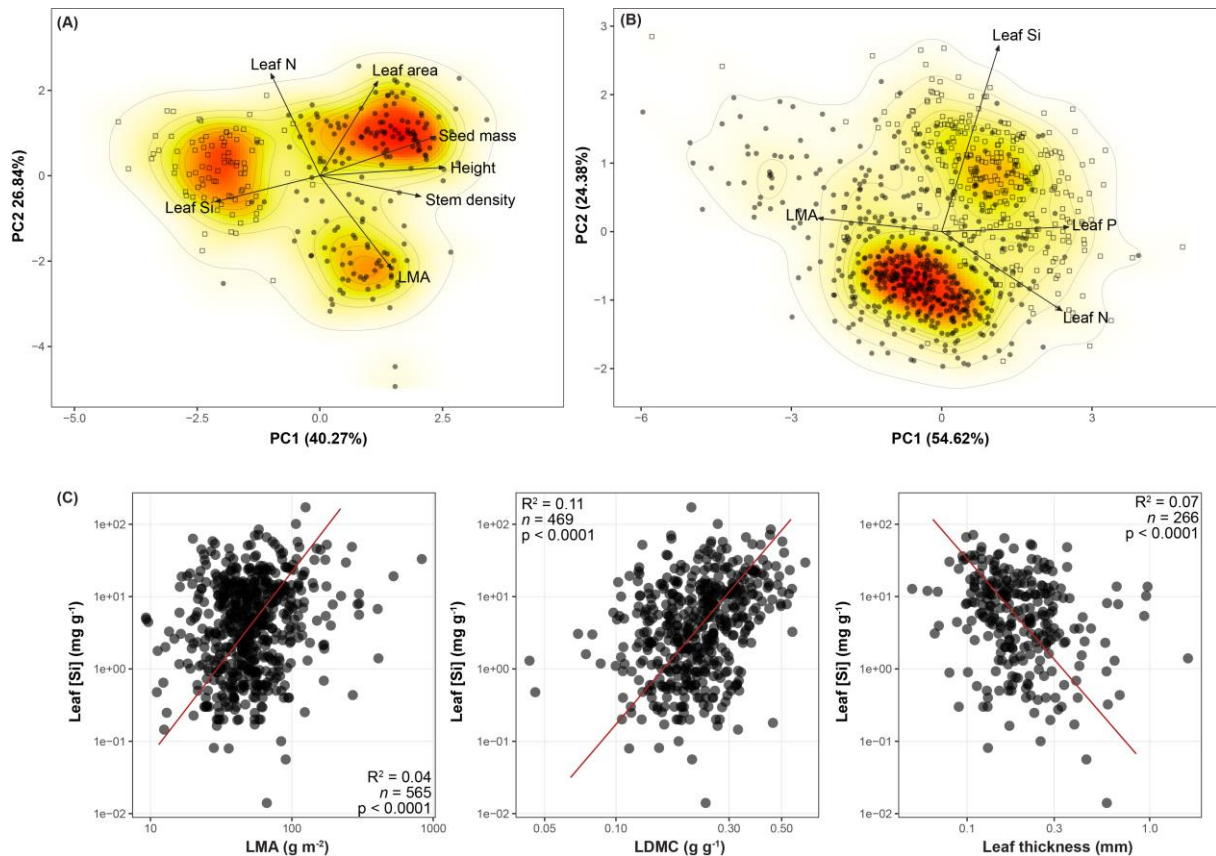
### 646 **Boxes (3)**

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

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

656 Cooke et al. [40] aimed to include leaf [Si] in the *leaf economics spectrum* (LES; [17]). They  
657 showed that species with shorter leaf lifespan generally exhibit higher leaf [Si], but did not  
658 identify correlations between leaf [Si] and other LES traits [40]. With more species, we found  
659 that leaf [Si] was significantly positively related with leaf [P],  $A_{\text{mass}}$  and  $A_{\text{area}}$  and significantly  
660 negatively related with leaf lifespan and LMA (Figure S3). However, leaf [Si] was independent  
661 of the LES (Figure IB), because of weak  $R^2$  (Figure S3) compared with the LES framework  
662 [17]. A fairly good relationship with  $A_{\text{mass}}$  was identified, however ( $R^2 = 0.19$ ;  $n = 454$ ).

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



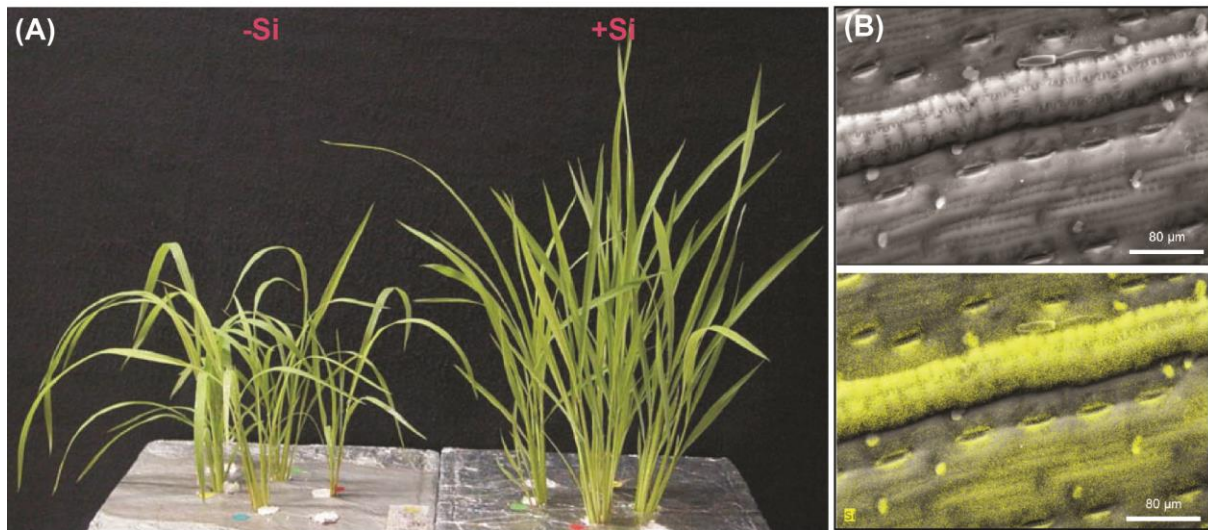
670

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

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

688 In grasses, Si has been linked to different plant architectural traits such as decreasing leaf  
689 insertion angle, increasing leaf straightness [44,121–123] and increasing plant height  
690 [46,67,123,124], as shown in Figure IIA. This has been attributed to the hardness of silica,  
691 which strengthens plant tissues, especially through silica deposits in cell walls [125,126]. In  
692 grasses, veins located on the abaxial epidermis made of fully silicified cells may also play a  
693 role in leaf erectness, as exemplified in sugarcane in Figure IIB [76]. Negative relationships  
694 between leaf [Si] and concentrations of C-based compounds have also been reported (*e.g.*,  
695 lignin, cellulose) which has reinforced the contention of a mechanical role of silicification, and  
696 has led to suggest “trade-offs” between Si and C components in leaves [4,44,100,127]. We  
697 found a significant negative relationship between leaf concentrations of Si and C of 838 species  
698 and driven by plant woodiness ( $R^2 = 0.24$ ; Figure S3), suggesting that non-woody species invest  
699 relatively more in Si than in C for leaf construction/defence compounds compared with woody  
700 species. After correcting leaf [C] for silica content, the relation is weaker but still highly  
701 significant ( $R^2 = 0.10$ ;  $p < 0.0001$ ), suggesting that dilution is not the only factor explaining the  
702 relationship between Si and C [30]. Nevertheless, the hypothesis of a Si-C trade-off requires  
703 more work at the cell and organ levels to better understand Si roles compared with C roles  
704 [100]. Future studies on Si and C-based components should pay specific attention to  
705 mechanisms underpinning the apparent trade-off [100].

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



716

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

722 **BOX 3. The costs of silicification in plants**

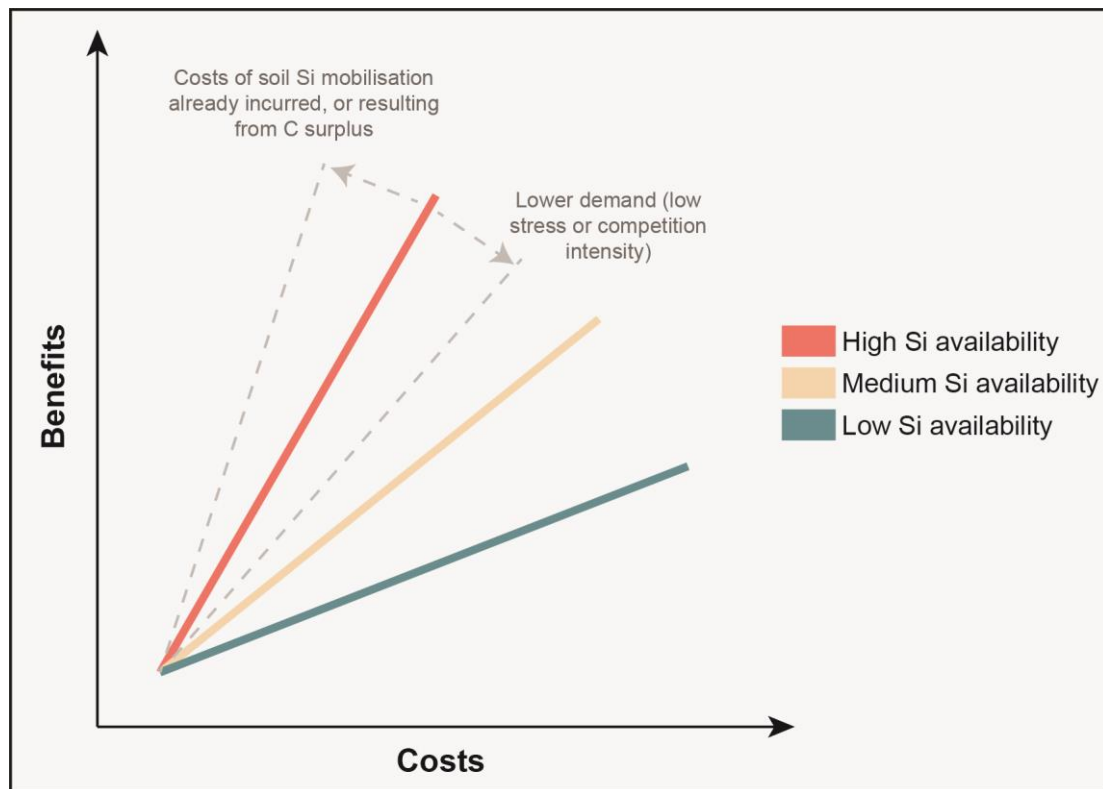
723 *Costs independent of soil Si availability* Transport of  $\text{Si}(\text{OH})_4$  into vascular plants has been  
 724 categorised as active, passive and rejective [130]. Passive transport involves  $\text{Si}(\text{OH})_4$  uptake in  
 725 the transpiration stream in the same  $\text{Si}(\text{OH})_4:\text{H}_2\text{O}$  ratio as occurs in the root medium. Active  
 726 uptake involves a higher, and rejective uptake a lower ratio. In *Oryza sativa*, active and passive  
 727 Si-uptake co-exist, and their relative contribution depends on external  $\text{Si}(\text{OH})_4$  concentrations  
 728 [130]. Active  $\text{Si}(\text{OH})_4$  uptake must occur at membrane(s) between medium and xylem sap,  
 729 because  $\text{Si}(\text{OH})_4$  concentrations in xylem exudates are more than 30 times higher than  
 730 concentrations in the root medium [131].

731 The known trans-plasmalemma proteins involved in  $\text{Si}(\text{OH})_4$  transport from the root medium  
 732 to the xylem catalyse influx (Lsi1) and efflux (Lsi2). Polar location of both Lsi1 (centrifugal)  
 733 and Lsi2 (centripetal) in *Oryza sativa* exodermis and endodermis suggests that the pathway of  
 734 **monosilicic acid** transport from exodermis to endodermis is apoplasmic [104,132]. In some  
 735 other plants, Lsi1 catalyses influx into epidermal and cortical cells, and Lsi2 catalyses efflux  
 736 from endodermal cells to the xylem [104,132]. Lsi1 catalyses  $\text{Si}(\text{OH})_4$  passive influx and Lsi2  
 737  $\text{H}^+$  antiport efflux with a 1 mol  $\text{H}^+:$ 1 mol  $\text{Si}(\text{OH})_4$  stoichiometry. With 1 mol  $\text{H}^+$  pumped per  
 738 mol ATP by the plasmalemma  $\text{H}^+$  pump [133], 1 mol ATP is needed per mol  $\text{Si}(\text{OH})_4$  leaving

739 a cell, so 2 mol ATP are required per mol  $\text{Si}(\text{OH})_4$  transferred from the root medium to the  
740 xylem sap of *Oryza sativa*. For plants with Lsi2 only in the endodermis, 1 mol ATP is required  
741 to move 1 mol  $\text{Si}(\text{OH})_4$  from the root medium to the xylem. Transport of  $\text{Si}(\text{OH})_4$  by Lsi1 occurs  
742 down a  $\text{Si}(\text{OH})_4$  concentration gradient from apoplasm to cytosol, with no other energisation,  
743 in agreement with the molecular structure of Lsi1 [134–136]. However, there is evidence of  
744 accumulation of  $\text{Si}(\text{OH})_4$  in the symplasm of root tips of *Oryza sativa* in both wildtype and an  
745 Lsi1 mutant [137], consistent with energised  $\text{Si}(\text{OH})_4$  transport at the plasma membrane not  
746 involving Lsi1. No evidence has been sought for the electrogenicity predicted for  $\text{H}^+$  antiport  
747 of Lsi2 by expression in *Xenopus* oocytes. For 2 mol ATP per mol  $\text{Si}(\text{OH})_4$  moved from the  
748 root medium to the xylem, the energy cost of producing a mol of the monomers of cell wall  
749 structural compounds, lignin and polysaccharide, is 13-fold and 7-fold, respectively, of that of  
750 the inorganic substitute,  $\text{SiO}_2$  [4]. This equivalence assumes that there is no energy cost of  
751 unloading  $\text{Si}(\text{OH})_4$  from xylem, or organic compounds associated with  $\text{SiO}_2$  deposits, and that  
752  $\text{SiO}_2$  /lignin or polysaccharide monomers are structurally equivalent.

753 *Costs dependent on soil Si availability* Previous calculations [4] have assumed assumed an  
754 inexhaustible supply of  $\text{Si}(\text{OH})_4$  which is not the case in many soils worldwide [105]. Si  
755 mobilisation from poorly-available forms, and plant Si uptake are significantly increased by  
756 release of root exudates (*e.g.*, carboxylates) and arbuscular mycorrhizal associations  
757 [38,109,138]. These nutrient-acquisition strategies are costly [101], and, therefore, Si  
758 accumulation involving rhizosphere processes would be significantly more expensive than  
759 currently acknowledged [38], as is the case for P and Fe [101,139]. We argue that costs of Si  
760 accumulation would largely depend on soil Si availability (Figure III). However, whether plants  
761 increase carboxylate secretion or their association with fungi – and are therefore spending  
762 energy – in responses to Si deficiency *itself* is unknown. The possibility of changes in root  
763 morphology, mycorrhizal symbionts, and root and mycorrhizal secretions related to deficiency  
764 of Si, rather than P or some other element, deserves further investigation [38,101]. Moreover,  
765 costs of carboxylates and other Si-mobilizing root exudates may be negligible if they have  
766 already been covered by other processes (*e.g.*, to mobilise soil P) or if they result from a C  
767 surplus under conditions of growth being limited by resources other than carbon supplied in  
768 photosynthesis [140,141] (Figure III). We call for more research at the rhizosphere level to  
769 answer these compelling questions.





770

771 **Figure III (Box 3).** Schematic representation of the costs and benefits of active Si accumulation  
 772 in plant organs as a function of soil Si availability. For a given soil and associated soil Si  
 773 availability, a lower demand for Si, as, for instance, in less stressful and/or competitive  
 774 environments, would decrease the benefits relative to the costs. Similarly, if costs of Si-  
 775 mobilizing root exudates (*e.g.*, carboxylates, phytosiderophores) have already been incurred to  
 776 mobilize other nutrients (*e.g.*, P or Fe) [38,101,139], or result from ‘free’ surplus carbon  
 777 [140,141], the benefits would increase relative to the costs.

## 778 Glossary

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

782 **Biomining:** process by which organisms form minerals

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

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

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

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

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

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

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

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

801 **Monosilicic acid:** soluble form of Si in soils, available for plant uptake, with the chemical  
802 formula  $\text{Si}(\text{OH})_4$

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

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

807 **Si transporter:** a transplasmalemma protein catalysing  $\text{Si}(\text{OH})_4$  transport into or out of cells

808 **Silica:** silicon dioxide, with the chemical formula  $\text{SiO}_2$ . Silica in plants is amorphous and  
809 hydrated:  $\text{SiO}_2 \cdot n\text{H}_2\text{O}$ . It may also contain other elements, including C

810 **Silicification:** process by which an organism incorporates soluble silicic acid  $\text{Si}(\text{OH})_4$  in the  
811 form of polymerised insoluble hydrated silica ( $\text{SiO}_2 \cdot n\text{H}_2\text{O}$ )