1 **Title**

2 Reviews and Syntheses: Impacts of plant silica - herbivore interactions on terrestrial biogeochemical

3 cycling

4 **Authors**

5 Bernice C. Hwang[1] and Daniel B. Metcalfe[1,2]

6 **Affiliations**

7 [1]Lund University, Department of Physical Geography and Ecosystem Science, Sölvegaten 12, Lund, 223 62,

8 Sweden.

9 [2]Umeå University, Department of Ecology and Environmental Science, Linnaeus väg 6, Umeå, 901 87,

10 Sweden.

11 **Correspondence**

12 Bernice C. Hwang

13 E-mail: bernice.hwang@nateko.lu.se

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Abstract

Researchers have known for decades that silicon plays a major role in biogeochemical and plant-soil processes in terrestrial systems. Meanwhile, plant biologists continue to uncover a growing list of benefits derived from silicon to combat abiotic and biotic stresses, such as defense against herbivory. Yet despite growing recognition of herbivores as important ecosystem engineers, many major gaps remain in our understanding of how silicon and herbivory interact to shape biogeochemical processes, particularly in natural systems. We review and synthesize 119 available studies directly investigating silicon and herbivory to summarize key trends and highlight research gaps and opportunities. Categorizing studies by multiple ecosystem, plant, and herbivore characteristics, we find substantial evidence for a wide variety of important interactions between plant silicon and herbivory, but highlight the need for more research particularly in non-graminoid dominated vegetation outside of the temperate biome as well as on the potential effects of herbivory on silicon cycling. Continuing to overlook silicon-herbivory dynamics in natural ecosystems limits our understanding of potentially critical animal-plant-soil feedbacks necessary to inform land management decisions and to refine global models of environmental change.

1 Introduction

For centuries researchers have intensively studied cycles of key nutrients influencing plant growth and diversity such as nitrogen (N) and phosphorus (P) across a diverse range of ecosystems (*e.g.*, Elser et al., 2007). Meanwhile, studies have often overlooked other nutrients such as silicon (Si), which is important for plant function and protection (Cooke et al., 2016) as well as for biogeochemical cycling (Street-Parrott and Barker, 2008). For instance, Si can reduce the impact of many abiotic and biotic pressures, including water, temperature and salinity stress, as well as nutrient deficiency, heavy metal toxicity, disease, and herbivory (Debona et al., 2017). Plants can likewise affect terrestrial silica fluxes by controlling weathering rates and activity of dissolved Si in soils and streams (Derry et al., 2005). Plants and their associated microbiota can accelerate the weathering of silicate minerals by altering the physical properties and reactivity of the soil environment (*e.g.*, pH, moisture, exposed surface area of minerals), and by taking up essential nutrients which destabilizes silicate minerals (Drever, 1994; Street-Parrott and Barker, 2008 and references therein). Since the silicate weathering process consumes carbon dioxide (CO_2) through chemical weathering of calcium- and magnesium-silicate minerals in continental rocks, the effects of plants on the Si cycle may influence the global carbon (C) cycle (Street-Perrott and Barker, 2008).

Plants take up dissolved Si from direct weathering of mineral silicates and biogenic Si released from leaf litter to soil (Cornelis and Delvaux, 2016), and Si in plants exceeds the concentrations of many plant macro-nutrients (Epstein, 1999). Si accumulation varies among species, with some plants containing only trace amounts, whereas Si can constitute up to 10% plant dry mass in "high Si accumulators" such as many grasses (Hodson et al., 2005). In the last decade, many studies have focused on agricultural systems (Guntzer et al., 2012; see also Fig. 1), in particular looking at grass species (*e.g.*, McNaughton et al., 1985; Hartley and DeGabriel, 2016), with fewer studies examining the role or importance of plant Si in natural (*i.e.*, non-agricultural and in the field) environments even though the degree of dissolved Si passed through ecosystems as filters can vary dramatically by biome (Cooke and Leishman, 2011; Schoelynck et al., 2014;

56 Cornelis et al., 2016; see also Fig 1). In natural systems, studies have focused on graminoid-dominated

57 vegetation types in the temperate biome, with relatively little research in tropical and boreal/subarctic

58 forest and herbaceous vegetation types, even though plant Si uptake and storage in these systems may be

59 significant (Cornelis et al., 2010; Katz, 2014).

60 Herbivory also creates a number of important feedbacks between plants and soils (Bardgett and Wardle,

61 2003). For example, invertebrate herbivores can supply a remarkably large amount of nutrients to tropical

62 and subarctic systems compared to other major sources, bringing likely labile nutrients to the forest floor

63 in the form of frass and bodies (Hartley and Jones, 2004; Metcalfe et al., 2014~~3~~; Kristensen et al., 2018).

64 Selective herbivory may also result in the dominance of plants that are nutrient poor and/or better

65 defended, which ultimately produces more recalcitrant litter that decomposes more slowly (Bardgett and

66 Wardle, 2003). Since plant Si is involved in plant defense (Debona et al., 2017), interactions between

67 herbivory and plant Si (Quigley and Anderson, 2016) may have the potential to exert a powerful influence

68 over ecosystem biogeochemistry and function.

69 There are multiple detailed reviews covering Si~~silicon~~ terrestrial biogeochemistry (*e.g.*, Conley, 2002;

70 Struyf and Conley, 2012) as well as Si-derived benefits to plants such as herbivore defense (*e.g.*, Frew et

71 al., 2018; Katz, 2019). However, given the likely importance of Si in multiple terrestrial biomes and the

72 strong evidence for a tight coupling between plant Si and herbivory, remarkably few studies have

73 investigated Si-herbivory dynamics in the context of biogeochemical cycling. Here, we review the role of

74 plant Si-herbivore dynamics in biogeochemical cycles in order to summarize existing knowledge and

75 emerging patterns, identify gaps in knowledge, and describe future research priorities. Towards this effort,

76 we surveyed available literature between 1900-2020 in the Web of Science core collection database using

77 search terms "silic*" and "herbivor*" and not "in silico" (314 results). We then filtered the results until

78 only those publications that directly studied Si and herbivory remained (119 publications), which we

79 categorized into various ecosystem, plant, and herbivore characteristics (Fig. 1). Our purpose is to identify

80 areas where this knowledge can be currently useful, such as agricultural and land management, and assist

81 efforts to better integrate potentially important but overlooked herbivore-plant-soil interactions into

82 global biogeochemical models to more accurately predict ecosystem function shifts in the face of

83 environmental change (Van der Putten et al., 2013).

84 **2 Silicon in terrestrial systems**

85 The biogeochemical Si cycle impacts global CO_2 concentrations through weathering silicate minerals and

86 transferring CO_2 from the atmosphere to the lithosphere (Conley, 2002). In terrestrial systems, soil is the

87 primary source of plant Si, with global variability of soil-forming factors (*e.g.*, parent rock, climate,

88 topography, age, biota) explaining the large variability in Si cycling rates (Cornelis et al., 2016). Many plant

89 species accumulate Si predominantly in leaves and needles as amorphous, biogenic silica, in large discrete

90 bodies known as phytoliths. Si then returns to the soil when plant material decomposes either as dissolved

91 Si, a quickly-available source of Si for terrestrial plants, or remain as as phytoliths, where C incorporated

92 by. phytoliths Carbon incorporated by phytoliths may accumulate in soils and sediments for hundreds to

93 thousands of years. For this reason, phytolith accumulation is considered as a key mechanism of

94 biogeochemical C sequestration (Parr and Sullivan, 2005). Plant-accumulated Si has been shown to reduce

95 the magnitude of Si released from terrestrial to aquatic ecosystems, thereby having direct implications on

96 Si availability in rivers and coastal waters, which could the influence diatom blooms and C uptake rates

97 (Coney et al., 2008, Carey and Fulweiler, 2012; see also Fig. 3b). Ultimately, terrestrial systems supply

98 approximately 78% of annual silica inputs to oceans (Tréguer and De La Rocha, 2013) and Si-accumulating

99 vegetation accounts for 55% of terrestrial net primary productivity (33 GtC per year), on par with the rate

100 that marine diatoms sequester C (Conley, 2002; Carey and Fulweiler, 2012).

101 Plants may preferentially use Si for certain functions such as structure and defense instead of C (Cooke

102 and Leishman, 2012) as Si can provide plants with structural support at a lower metabolic cost than C

103 (Raven, 1983). In some cases, Si is negatively correlated with lignin and cellulose content, possibly

104   contributing to plant structural support, and phenol content (Schoelynck et al., 2010; Cooke and Leishman,

105   2012). Intermediate Si fertilization additions, for example, have enhanced aboveground growth for crops

106   and reeds, possibly due to a partial substitution of organic C compounds by Si in plant tissue (Schaller et

107   al., 2012; Neu et al., 2017).

108   Soil Si may also facilitate the acquisition and release of other essential plant nutrients. For example, a

109   laboratory experiment demonstrated that silicon addition significantly increased P mobilization in a variety

110   of arctic soils (Schaller et al., 2019). Researchers have found that Si can also increase plant N use efficiency

111   while decreasing C and increasing P in grasslands (Neu et al., 2017) and affect the calcium (Ca) content of

112   grasses (Brackhage et al., 2013). The abundance of certain plant functional groups (*e.g.*, Si-rich grasses) in

113   plant communities can affect Si and Ca biogeochemistry as a result of differences in elemental

114   concentrations among plant species and related effects on nutrient cycling via processes such as

115   decomposition (Schaller et al., 2016). The potential of Si to affect plant growth and elemental

116   stoichiometry in grasslands can, by extension, then affect biogeochemical cycles (Schaller et al., 2017).

117   Changes in plant nutrient stoichiometry due to Si may have broad implications for other natural systems,

118   where the (un)availability of essential nutrients can shape the productivity, composition, diversity,

119   dynamics and interactions of plant, animal, and microbial populations (Vitousek, 2010). For example, P can

120   be limiting in weathered tropical forest soils (Vitousek, 2010), so changes in P availability due to Si (Neu et

121   al., 2017) can have concomitant effects on productivity. Furthermore, the recycling of Si within forests

122   impacts continental Si cycling, especially in tropical forests which take up Si at a faster rate in terms of

123   mass per unit ground area than other biomes, particularly in highly weathered soils (Alexandre et al., 1997;

124   Cornelis et al., 2016; Schaller et al., 2018). Notably, unlike major plant nutrients for which foliar

125   concentrations significantly decreased with increasing soil age, foliar Si concentrations continually

126   increased with increasing soil age in two Australian soil chronosequences (de Tombeur et al., 2020).

127 Returning phytoliths to topsoil can result in the slow-release of Si that sustains the terrestrial cycle during

128 ecosystem retrogression.

129 A summary of literature shows that studies of Si-herbivore dynamics have focused on the ecology and

130 physiology of Si in the grass family (Fig. 1), *Poaceae*, which includes many species that accumulate large

131 amounts of Si in their tissues. Species richness can increase plant Si stocks via its positive relationship with

132 biomass production but can have a negative effect on Si concentration in the aboveground biomass, which

133 may influence processes such as decomposition, nutrient cycling and herbivory (Schaller et al., 2016).

134 Some studies indicate Si content of plant litter may be positively correlated to decomposition rate (*e.g.*,

135 Schaller et al., 2013). Because plant-stored Si releases Si into soils and sediments relatively rapidly, high Si-

136 accumulating plants like grasses can influence Si turnover rates in ecosystems by uptake, storage, and

137 release of Si during plant decomposition (Schaller et al., 2016 and references therein).

138 However, several non-monocot angiosperms also store significant foliar Si (Hodson et al., 2005), and

139 variation in foliar Si can play important roles such as in plant defense and metal toxicity reduction even for

140 low-accumulators (Katz, 2014 and references therein). Si contents vary by as much as 2-3 orders of

141 magnitude among plant families, orders and phyla (Hodson et al., 2005), and grass-rich systems tend to

142 be richer in Si and more productive than systems without grasses (Carey and Fulweiler, 2012). However,

143 nutrient use strategies can vary intra-specifically across environmental gradients at least within controlled

144 settings (Harley and DeGabriel, 2016 and references therein). ~~Therefore, we need more field-based~~

145 ~~information about how Si content varies along large-scale environmental gradients to improve global~~

146 ~~biogeochemistry models.~~

147 Anthropogenic perturbations, such as agriculture, deforestation, urbanization, and climate warming, can

148 also have profound effects on terrestrial silica biogeochemistry (Conley et al., 2008; Struyf and Conley,

149 2012; Carey and Fulweiler, 2016; Gewirtzman et al., 2019). Deforested areas can increase soil erosion,

150 resulting in the loss of high biogenic Si concentrations found in surface soils (Saccone et al., 2007). Urban

areas have limited ability to take up dissolved Si into vegetation and agricultural lands retain less biogenic Si as it is frequently removed through harvesting and may not be replenished by vegetation-stimulated silicate weathering (Struyf and Conley, 2012; Vandevenne et al., 2012). Global agricultural Si export from harvesting is estimated to be 223 kg Si yr^{-1} (Matichenkov and Bocharnikova, 2001) compared to the 142 kg Si yr^{-1} total quantity of dissolved Si transferred from continents to oceans by rivers (Tréguer et al., 1995). In addition, soil warming due to climate change can increase the extent of internal Si recycling in temperate forests (Gewirtzman et al., 2019) and changes in precipitation intensity, as expected with climate change, can increase surface run-off and top-soil erosion reducing biogenic Si in surface soils (Conley et al., 2008; Struyf et al., 2010). ~~Thus, researchers should take into account the potential impact of land-use and climate changes on terrestrial Si fluxes when modeling terrestrial Si mobilization.~~

3 Effects of silicon on herbivory

Si is known to defend plants against a wide range of biotic stresses, including pathogen infection and herbivory (Reynolds et al., 2009; Guntzer et al., 2012; Frew et al., 2018 and references therein). Si-mediated defenses against herbivores involve both direct and indirect physical or mechanical barriers, as well as indirect biochemical or molecular mechanisms (Fig. 2). In addition, plant communities with high Si can affect herbivore communities. Plant groups with high leaf toughness, high Si concentrations, and low leaf nitrogen concentrations, for example, can also be associated with decreased grassland herbivore species richness (Schuldt et al., 2019). Furthermore, studies have reported how grass Si content can drive herbivore populations, which may be synchronized with plant Si content cycles (Massey et al., 2008; Hartley, 2015).

Si-derived mechanical barriers are often thought to effectively shorten the duration of attack, both directly or indirectly, by making tissues more difficult to chew, penetrate, and digest (Hunt et al., 2008; Massey and Hartley, 2009), and increasing exposure time to predators (Massey and Hartley, 2009). For example, discrete silica bodies in and on the surface of leaves can reduce herbivory (Hartley et al., 2015). Si

175 structures may wear down herbivore mouthparts (Massey and Hartley, 2009), affecting herbivore

176 ingestion and nutrition (Frew et al., 2018; Hunt et al., 2008). These abrasive phytoliths can also lacerate

177 herbivore body parts or facilitate pathogen transmission into herbivores (Lev-Yadun and Halpern, 2019).

178 Si may also alter nutritional quality indirectly via changes to foliar C : N ratio and P concentrations (Frew

179 et al., 2018) while plant nutrient status may influence the overall efficacy of Si-based defenses against

180 herbivory (Mosie et al., 2019). As a consequence, some herbivores demonstrate low preference for Si-rich

181 plants and slower growth rates when feeding on Si-rich diets (Massey and Hartley, 2006, 2009).

182 Several studies have documented effects of soil Si addition on plant chemical defenses (*e.g.*, Reynolds et

183 al., 2009), anti-herbivore phytohormonal signaling (*e.g.*, Hall et al., 2019), and changes in plant nutritional

184 quality (*e.g.*, Frew et al., 2018; Moise et al., 2019). For example, Si may induce indirect defense

185 mechanisms by altering the composition of herbivore-induced plant volatiles that attract herbivore

186 parasitoids and predators (Liu et al., 2017). Some studies also point to effects of Si on plant secondary

187 metabolism and gene expression in plant development and defense (Markovich et al., 2017; Frew et al.,

188 2018 and references therein). But because Si has relatively limited chemical reactivity, its role on plant

189 chemical changes may be indirect rather than direct (Coskun et al., 2019). For example, effectors released

190 by insects could be trapped within the extracellular Si matrix, precluding them from deregulating the plant

191 defense response, or from recognizing the plant as a suitable host (Coskun et al., 2019).

192 While researchers continue to debate the biological roles of Si and uncover the mechanisms behind them

193 (Frew et al., 2018; Coskun et al., 2019), we conclude that, at a minimum, Si mitigates the negative impacts

194 of various stressors, such as herbivory, which then enable plants to improve growth potential (Johnson et

195 al., 2019).

196 **4 Effects of herbivory on plant silicon**

197 Of the 119 reviewed studies, the majority of Si-herbivory publications have focused on insects that damage

198 shoots (68), while other animals including mammals (35), and insects from other feeding guilds (14), are

199 less frequently represented (Fig. 1). While many studies in the literature review investigate the effects of

200 Si on herbivory (114), few studies focus on the effects of herbivory on Si (5). Though few, these studies

201 show that herbivores can also induce Si uptake and accumulation by plants in response to herbivore attack

202 (Massey et al., 2007; Hartley and Gabriel, 2016). Although how much Si uptake is induced may depend on

203 plant species, herbivore type, and environmental conditions, the degree of induction can be positively

204 correlated with herbivory duration or frequency (Soininen et al., 2013). In one study, the Si content of two

205 species of grasses that experienced repeated damage by voles and locusts was 2-4 times more than

206 individuals of the same species that experienced only one damage event (Massey et al., 2007). Some grass

207 species have been shown to have as much as twice the Si contents in more heavily grazed localities

208 (Brizuela et al., 1986). However, one study investigating grazing effects on Si yielded different results. In a

209 saltmarsh, Si export rates at sheep-grazed sites were actually lower than at ungrazed sites (Müller et al.,

210 2013). Variable responses between different grasslands underscore the need for wider sampling to study

211 Si-herbivory dynamics in different ecosystems with their unique characteristics.

212 **4.1 Potential effects of herbivory on terrestrial silicon cycling**

213 While multiple reviews synthesize terrestrial Si biogeochemical cycling (*e.g.*, Conley, 2002; Struyf and

214 Conley, 2012) and effects of Si on herbivory (*e.g.*, Debona et al., 2017; Frew et al., 2018), few studies have

215 explored the potential effects of herbivory on Si cycling. Variation in Si accumulation and deposition

216 associated with herbivory, Si availability, and environmental variables could have important implications

217 for Si cycling (Cooke and DeGabriel, 2016 and references therein). Herbivores can distribute large

218 quantities of resources across the landscape, having important effects on nutrient cycling and ecosystem

219 productivity (Metcalfe et al., 2014; Bakker et al., 2016). Schoelynck et al. (2019), for example, found that

220 hippos contribute 32% to the biogenic Si flux and more than 76% to the total Si flux in a savannah-river

221   system. ~~We estimate that Si fluxes via the herbivory pathway can meet or exceed other major sources of~~

222   ~~Si, although flux information on some major habitat types is missing~~Bringing together published Si flux

223   data with estimates of herbivory for the first time, we estimate that Si fluxes via the herbivory pathway

224   could meet or exceed other major sources of Si (Table 1), although flux information on some major habitat

225   types is missing. Herbivores may also influence Si pathways by making more labile forms of Si available.

226   For example, Vandevenne et al. (2013), found that grazing by cattle can increase reactivity and

227   dissolvability of biogenic Si after digestion, leading to higher Si turnover rates and mobilization potential

228   (2 versus 20 kg Si ha^{-1} y^{-1}). Greater Si mobilization terrestrially due to herbivory can potentially affect the

229   uptake of Si by plants as well as the movement of other linked nutrients indirectly (Fig. 3). It is, however,

230   currently unclear whether the more mobilized Si is ~~then~~ absorbed by vegetation, taken up by microbes, or

231   exported from the system ~~(Fig. 3)~~. Future research could follow the fate of more mobilized Si derived from

232   herbivores, which may depend on local biotic and abiotic conditions such as soil properties or

233   plant/microbial composition. In a wetland study, litter decomposition by heterotrophic microbes was

234   significantly influenced by the Si availability during plant growth, whereby litter decomposition rates were

235   positively correlated with higher Si content (Schaller et al., 2013). In other words, potentially greater

236   export and plant uptake of biogenic Si due to herbivory may impact decomposition and nutrient cycling in

237   some systems. Grasslands demonstrate a high capacity to store biogenic Si as well as transport Si from

238   relatively inert mineral silicate soil layers to biologically active soil layers (Blecker et al., 2006). If grazing

239   can change the distribution and reactivity of Si in grasslands, herbivory may alter Si turnover and export

240   at rates important to estimate for Si cycling in other agricultural and natural systems as well.

241   Understanding the role of herbivores in mobilizing Si may have important implications for land

242   management.

243   Researchers have found that even small shifts in terrestrial biogenic Si reactivity could alter the balance

244   between Si storage and export from ecosystems (Struyf and Conley, 2012). Herbivory may increase

245 dissolved Si mobility (Vandevenne et al., 2013), and, if absorbed by plants, thereby decrease C uptake

246 (Cooke and Leishman, 2012), increase N use efficiency, and increase P uptake of plants (Neu et al., 2017;

247 also see Fig. 3). Grassland herbivores may also preferentially consume plants with less Si (Massey and

248 Hartley, 2006), potentially influencing ecosystem Si cycling and plant community dynamics (Garbuzov et

249 al., 2011). Combined with Si-mediated changes in plant nutrient stoichiometry and efficiency (Neu et al.,

250 2017), these findings highlight the need for more field research on how herbivory-Si interactions impact

251 community- and ecosystem-level processes.

252 **6~~5~~ Conclusions**

253 Our analysis has shown the magnitude of impact of plant Si on herbivore populations and the potential

254 impact of herbivores on Si fluxes~~We have begun to understand the magnitude of impact of plant Si on~~

255 ~~herbivore populations and the potential impact of herbivores on Si fluxes~~, which may have important

256 agricultural and land management implications. In an effort to improve land management decisions and

257 projections of biogeochemical cycling to future climate and land-use changes, however, we need to

258 expand our understanding of Si-herbivore dynamics. Long-standing research makes it clear that Si plays an

259 important role in both biogeochemistry cycling and herbivory but major knowledge gaps remain. Based

260 upon our review we highlight the following future research priorities:

261 - Fate of more mobilized Si as a result of herbivory in agricultural settings.

262 - How Si-herbivory dynamics operate beyond crops in controlled or agricultural settings.

263 - Si-herbivore dynamics in herbivore feeding guilds other than shoot feeders.

264 - Impact of herbivory on biogeochemical cycling in natural settings, which remain understudied but

265 where evidence indicates that Si can cycle at a high rate and herbivory is an important ecosystem

266 process.

267 • Field-based studies on Si-herbivory dynamics along key environmental gradients by different
268 herbivore feeding guilds.

269 Given the demonstrated importance of Si and herbivores, and the relative paucity of information on their
270 interaction particularly in natural, non-graminoid dominated systems, we believe this information is
271 critical to generating more accurate model representations of animal-plant-soil feedbacks, and their
272 impacts upon ecosystem processes in different terrestrial systems.

273 **Data Availability**

274 The list of publications reviewed and classified for this article can be found at doi:
275 10.6084/m9.figshare.12026997.

276 **Authors' Contributions**

277 BH and DM conceived the ideas and designed methodology; BH collected and synthesized the data. With
278 input from DM, BH led the writing of the manuscript. Both authors contributed critically to the drafts and
279 gave final approval for publication.

280 **Competing Interests**

281 The authors declare that they have no conflict of interest.

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285 **References**

286 Alexandre, A., Meunier, J.-D., Lézine A.-M., Vincens, A., and Schwartz, D.: Phytoliths: indicators of grassland
287 dynamics during the late Holocene in intertropical Africa, Palaeogeogr. Palaeocl., 136(1-4), 213–229,
288 https://doi.org/10.1016/s0031-0182(97)00089-8, 1997.

Bakker, E. S., Pages, J. F., Arthur, R., and Alcoverro, T.: Assessing the role of large herbivores in the structuring and functioning of freshwater and marine angiosperm ecosystems, Ecography, 39, 162–179, https://doi.org/10.1111/ecog.01651, 2016.

Bardgett, R. D. and Wardle, D. A.: Herbivore-Mediated Linkages between Aboveground and Belowground Communities, Ecology, 84, 2258-2268, https://doi.org/ 10.1890/02-0274, 2003.

Bartoli, F., The biogeochemical cycle of silicon in two temperate forest ecosystems, Ecol. Bull., 469-476, https://doi.org/10.2307/20112881, 1983.

Blecker, S. W., McCulley, R. L., Chadwick, O. A., and Kelly, E. F.: Biologic cycling of silica across a grassland bioclimosequence, Global Biogeochem. Cy., 20, GB3023, https://doi.org/10.1029/2006gb002690, 2006.

Brackhage, C., Schaller, J., Bäucker, E., and Dudel, E. G.: Silicon availability affects the stoichiometry and content of calcium and micro nutrients in the leaves of Common Reed, Silicon, 5, 199–204, https://doi.org/ 10.1007/s12633-013-9145-3, 2013.

Brizuela, M. A., Detling, J. K., and Cid, M, S.: Silicon concentration of grasses growing in sites with different grazing histories, Ecology, 67, 1098-1101, https://doi.org/10.2307/1939834, 1986.

Carey, J. C. and Fulweiler, R. W.: The Terrestrial Silica Pump, PLoS ONE, 7, e52932, https://doi.org/10.1371/journal.pone.0052932, 2012.

Carey, J. C. and Fulweiler, R. W.: Human appropriation of biogenic silicon – the increasing role of agriculture, Funct. Ecol., 30, 1331–1339, https://doi.org/10.1111/1365-2435.12544, 2016.

Cebrian, J.: Role of first-order consumers in ecosystem carbon flow, Ecol. Lett., 7, 232-240, https://doi.org/10.1111/j.1461-0248.2004.00574.x, 2004.

Conley, D. J.: Terrestrial ecosystems and the global biogeochemical silica cycle, Global Biogeochem. Cy., 16, 68–1–68–8, https://doi.org/10.1029/2002gb001894, 2002.

311   Conley, D. J., Likens, G. E., Buso, D. C., Saccone, L., Bailey, S. W., and Johnson, C. E.: Deforestation causes

312   increased dissolved silicate losses in the Hubbard Brook Experimental Forest, Glob. Change Biol., 14, 2548–

313   2554, https://doi.org/10.1111/j.1365-2486.2008.01667.x, 2008.

314   Cooke, J. and Leishman, M. R.: Is plant ecology more siliceous than we realize?, Trends Plant Sci., 16, 61–

315   68, https://doi.org/10.1016/j.tplants.2010.10.003, 2011.

316   Cooke, J. and Leishman, M. R.: Tradeoffs between foliar and carbon-based defences: evidence from

317   vegetation   communities   of   contrasting   soil   types,   Oikos,   121,   2052–2060,   https://doi-

318   org.ludwig.lub.lu.se/10.1111/j.1600-0706.2012.20057.x, 2012.

319   Cooke, J., and DeGabriel J. L.: Editorial: Plant Silicon Interactions between Organisms and the Implications

320   for Ecosystems, Front. Plant Sci. 7, 1001, https://doi.org/10.3389/fpls.2016.01001, 2016.

321   Cooke, J., DeGabriel, J. L., and Hartley, S. E.: The functional ecology of plant silicon: geoscience to genes,

322   Funct. Ecol., 30, 1270–1276, https://doi.org/10.1111/1365-2435.12711, 2016.

323   Cornelis, J. T. and Delvaux, B.: Soil processes drive the biological silicon feedback loop, Funct. Ecol., 30,

324   1298–1310, https://doi.org/10.1111/1365-2435.12704, 2016.

325   Cornelis, J., Ranger, J., Iserentant, A., and Delvaux, B.: Tree species impact the terrestrial cycle of silicon

326   through   various   uptakes,   Biogeochemistry,   97,   231–245,   https://doi-

327   org.ludwig.lub.lu.se/10.1007/s10533-009-9369-x, 2010.

328   Coskun, D., Deshmukh, R., Sonah, H., Menzies, J. G., Reynolds, O. L., Ma, J. F., Kronzucker, H. J., and

329   Bélanger, R. R.: The controversies of silicon's role in plant biology, New Phytol., 221, 67–85,

330   https://doi.org/ 10.1111/nph.15343, 2019.

331 De Tombeur, F., Turner, B. L., Laliberte, E., Lambers, H., Mahy, G., Faucon, M.-P., Zeminuk, H., and Cornelis,

332 J. T.: Plants sustain the terrestrial silicon cycle during ecosystem retrogression, Science, 369, 1245-1248,

333 https://doi.org/10.1126/science.abc0393, 2020.

334 Debona, D., Rodrigues, F. A., and Datnoff, L. E.: Silicon's role in abiotic and biotic plant stresses, Annu. Rev.

335 Phytopathol., 55, 85–107, https://doi.org/10.1146/annurev-phyto-080516-035312, 2017.

336 Derry, L. A., Kurtz, A. C., Ziegler, K., and Chadwick, O. A.: Biological control of terrestrial silica cycling and

337 export fluxes to watersheds, Nature, 433, 728–731, https://doi.org/10.1038/nature03299, 2005.

338 Drever, J. I.: The effect of land plants on weathering rates of silicate minerals, Geochimica et Cosmochimica

339 Acta, 58, 2325–2332, https://doi.org/10.1016/0016-7037(94)90013-2, 1994.

340 Elser, J. J., Bracken, M. E. S., Cleland, E. E., Gruner, D. S., Harpole, W. S., Hillebrand, H., Ngai, J. T., Seabloom,

341 E. W., Shurin J. B., and Smith, J. E.: Global analysis of nitrogen and phosphorus limitation of primary

342 producers in freshwater, marine and terrestrial ecosystems, Ecol. Lett., 10, 1135–1142,

343 https://doi.org/10.1111/j.1461-0248.2007.01113.x, 2007.

344 Epstein, E.: Silicon, Annu. Rev. Plant Phys., 50, 641–664,

345 https://doi.org/10.1146/annurev.arplant.50.1.641, 1999.

346 Frew, A., Weston, L. A., Reynolds, O. L., Gurr, G. M.: The role of silicon in plant biology: a paradigm shift in

347 research approach, Ann. Bot., 121, 1265–1273, https://doi.org/10.1093/aob/mcy009, 2018.

348 Garbuzov, M., Reidinger, S., and Hartley, S.: Interactive effects of plant-available soil silicon and herbivory

349 on competition between two grass species, Ann. Bot., 108, 1355–1363,

350 https://doi.org/10.1093/aob/mcr230, 2011.

351 Gewirtzman, J., Tang, J., Melillo, J. M., Werner, W. J., Kurtz, A. C., Fulweiler, R. W., and Carey, J. C.: Soil

352 Warming Accelerates Biogeochemical Silica Cycling in a Temperate Forest, Front. Plant Sci., 10, 1097,

353 https://doi.org/10.3389/fpls.2019.01097, 2019.

354 Guntzer, F., Keller, C., and Meunier, J. D.: Benefits of plant silicon for crops: a review, Agron. Sustain. Dev.,

355 32, 201–213, https://doi.org/10.1007/s13593-011-0039-8, 2012.

356 Hall, C. R., Waterman J. M., Vandegeer, R. K., Hartley, S. E., and Johnson, S. N.: The Role of Silicon in

357 Antiherbivore Phytohormonal Signalling. Front. Plant Sci., 10, 1132,

358 https://doi.org/10.3389/fpls.2019.01132, 2019.

359 Hartley, S. E.: Round and round in cycles? Silicon-based plant defences and vole population dynamics,

360 Funct. Ecol., 29, 151-153, https://doi.org/10.1111/1365-2435.12365, 2015.

361 Hartley, S. E. and DeGabriel, J. L.: The ecology of herbivore-induced silicon defences in grasses, Funct. Ecol.,

362 30, 1311–1322, https://doi.org/10.1111/1365-2435.12706, 2016.

363 Hartley, S. E. and Jones, T. H.: Insect herbivores, nutrient cycling and plant productivity, In Insects and

364 ecosystem function (eds. Weisser, W.W., Siemann, E.), Springer-Verlag, Heidelberg, Germany, 27–46,

365 https://doi.org/10.1007/978-3-540-74004-9_2, 2004.

366 Hartley, S. E., Fitt, R. N., McLarnon, E. L., and Wade, R. N.: Defending the leaf surface: intra- and inter-

367 specific differences in silicon deposition in grasses in response to damage and silicon supply, Front. Plant

368 Sci., 6, 35, https://doi.org/10.3389/fpls.2015.00035, 2015.

369 Hodson, M. J., White, P. J., Mead, A., and Broadley, M. R.: Phylogenetic variation in the silicon composition

370 of plants, Ann. Bot., 96, 1027–1046, https://doi.org/10.1093/aob/mci255, 2005.

371 Johnson, S. N., Rowe R. C., and Hall C. R.: Silicon is an inducible and effective herbivore defence against

372 *Helicoverpa punctigera* (Lepidoptera: *Noctuidae*) in soybean, B. Entomol. Res., 1–6,

373 https://doi.org/10.1017/s0007485319000798, 2019.

374 Katz, O.: Beyond grasses: the potential benefits of studying silicon accumulation in non-grass species,

375 Front. Plant Sci., 5, 376, https://doi.org/10.3389/fpls.2014.00376, 2014.

376 Katz, O.: Silicon content is a plant functional trait: implications in a changing world, Flora, 254, 88-94,

377 https://doi.org/10.1016/j.flora.2018.08.007, 2019.

378 Kristensen, J. A., Metcalfe, D. B., and Rousk, J. The biogeochemical consequences of litter transformation

379 by insect herbivory in the subarctic: a microcosm simulation experiment, Biogeochemistry, 138, 323–336,

380 https://doi.org/10.1007/s10533-018-0448-8, 2018.

381 Lev-Yadun, S. and Halpern, M.: Extended phenotype in action. Two possible roles for silica needles in

382 plants: not just injuring herbivores but also inserting pathogens into their tissues, Plant Signaling and

383 Behavior, 1–5, https://doi.org/10.1080/15592324.2019.1609858, 2019.

384 Liu, J., Zhu, J., Zhang, P., Han, L., Reynolds, O. L., and Zeng, R., Wu, J., Shao, Y., You, M., and Gurr G.

385 M.: Silicon Supplementation Alters the Composition of Herbivore Induced Plant Volatiles and Enhances

386 Attraction of Parasitoids to Infested Rice Plants, Front. Plant Sci., 8, 1265,

387 https://doi.org/10.3389/fpls.2017.01265, 2017.

388 Markovich, O., Steiner, E., Kouřil, Š., Tarkowski, P., Aharoni, A., and Elbaum, R.: Silicon promotes cytokinin

389 biosynthesis and delays senescence in Arabidopsis and Sorghum, Plant Cell Environ., 40, 1189–1196,

390 https://doi.org/10.1111/pce.12913, 2017.

391 Massey, F. P. and Hartley, S. E.: Experimental demonstration of the antiherbivore effects of silica in grasses:

392 impacts on foliage digestibility and vole growth rates, Proc. R. Soc. Lond. B Biol. Sci., 273, 2299–2304,

393 https://doi.org/10.2307/25223602, 2006.

Massey, F. P. and Hartley, S. E.: Physical defences wear you down: progressive and irreversible impacts of silica on insect herbivores, J. Anim. Ecol., 78, 281–291, https://doi.org/10.1111/j.1365-2656.2008.01472.x, 2009.

Massey, F. P., Ennos, A. R., and Hartley, S. E.: Herbivore specific induction of silica-based plant defences, Oecologia, 152, 677-683, https://10.1007/s00442-007-0703-5, 2007.

Massey, F. P., Smith, M. J., Lambin, X., and Hartley, S. E.: Are silica defences in grasses driving vole population cycles?, Biol. Lett., 4, 419-422, https://doi.org/10.1098/rsbl.2008.0106, 2008.

Matichenkov, V. V., Bocharnikova, E. A.: The relationship between silica and soil physical and chemical properties, In Silica in agriculture (eds.: Datnoff, L. E., Snyder, G. H., and Korndörfer, G. H.), Amsterdam, Netherlands: Elsevier, https://doi.org/10.1016/S0928-3420(01)80017-3, 2001.

McNaughton S. J., Tarrants, J. L., McNaughton, M. M., and Davis, R. H.: Silica as a defense against herbivory and a growth promoter in African grasses, Ecology, 66, 528-535, https://doi-org.ludwig.lub.lu.se/10.2307/1940401Citations: 169, 1985.

Metcalfe, D. B., Asner, G. P., Martin, R. E., Silva Espejo, J. E., Huasco, W. H., Farfán Amézquita, F. F., Javier E. Silva Espejo Walter Huaraca Huasco Felix F. Farfán Amézquita, Carranza-Jimenez, L., Galiano Cabrera, D. F., Durand Baca, L., Sinca, F., Huaraca Quispe, L. P, Alzamora Taype, I., Eguiluz Mora, L., Rozas Dávila, A., Mamani Solórzano, M., Puma Vilca, B. L., Laupa Román, J. M., Guerra Bustios, P. C., Salinas Revilla, N., Tupayachi, R., Girardin, C. A. J., Doughty, C. E., and Yadvinder, M.: Herbivory makes major contributions to ecosystem carbon and nutrient cycling in tropical forests, Ecol. Lett., 17, 324–332, https://doi-org.ludwig.lub.lu.se/10.1111/ele.12233, 2014.

Moise, E. R. D, McNeil, J. N., Hartley, S. E., Henry, H. A. L.: Plant silicon effects on insect feeding dynamics are influenced by plant nitrogen availability, Entomol. Exp. Appl., 167, 91-97, https://doi.org/10.1111/eea.12750, 2019.

417 Müller, F., Struyf, E., Hartmann, J., Weiss, A., and Jensen, K. L.: Impact of grazing management on silica

418 export dynamics of Wadden Sea saltmarshes, Estuar. Coast. Shelf Sci., 127, 1–11, https://

419 10.1016/j.ecss.2013.03.010, 2013.

420 Neu, S., Schaller, J., and Dudel, E. G.: Silicon availability modifies nutrient use efficiency and content, C:N:P

421 stoichiometry, and productivity of winter wheat (*Triticum aestivum L.*), Sci. Rep., 7, 40829, https://doi.org/

422 10.1038/srep40829, 2017.

423 Parr, J. F., Sullivan, L. A.: Soil carbon sequestration in phytoliths, Soil Biol. Biochem., 37, 117–124,

424 https://doi.org/10.1016/j.soilbio.2004.06.013, 2005.

425 Quigley, K. M., Donati, G. L., and Anderson, T. M.: Variation in the soil "silicon landscape" explains plant

426 silica accumulation across environmental gradients in Serengeti, Plant Soil, 410, 217–229,

427 https://doi.org/10.1007/s11104-016-3000-4, 2016.

428 Raven, J. A.: The transport and function of silicon in plants, Biol. Rev. 58, 179-207, doi:10.1111/j.1469-

429 185x.1983.tb00385.x, 1983.

430 Reynolds, O. L., Keeping, M. G., and Meyer, J. H.: Silicon-augmented resistance of plants to herbivorous

431 insects: a review, Ann. Appl. Biol., 155, 171–186, https://doi.org/10.1111/j.1744-7348.2009.00348.x,

432 2009.

433 Saccone, L., Conley, D. J., Koning, E., Sauer, D., Sommer, M., Kaczorek, D., Blecker, S. W., and Kelly, E. F.*:*

434 Assessing the extraction and quantification of amorphous silica in soils of forest and grassland ecosystems,

435 Eur. J. Soil Sci. 58, 1446–1459, https://doi.org/10.1111/j.1365-2389.2007.00949.x, 2007.

436 Schaller, J. and Struyf, E.: Silicon controls microbial decay and nutrient release of grass litter during aquatic

437 decomposition, Hydrobiologia, 709, 201– 212, https://doi.org/10.1007/s10750-013-1449-1, 2013.

438 Schaller, J., Faucherre, S., Joss, H., Obst, M., Goeckede, M., Planer-Friedrich, B. Peiffer, S., Gilfedder, B.,

439 and Elberling, B.: Silicon increases the phosphorus availability of Arctic soils, Sci. Rep.-UK, 9, 449,

440 https://doi.org/10.1038/s41598-018-37104-6, 2019.

441 Schaller, J., Hodson, M. J., Struyf, E.: Is relative Si/Ca availability crucial to the performance of grassland

442 ecosystems?, Ecosphere, 8, e01726, https://doi.org/10.1002/ecs2.1726, 2017.

443 Schaller J., Roscher, C., Hillebrand, H., Weigelt, A., Oelmann, Y., Wilcke, W., Ebeling, A., and Weisser, W.

444 W.: Plant diversity and functional groups affect Si and Ca pools in aboveground biomass of grassland

445 systems, Oecologia, 182, 277–286, https://doi.org/10.1007/s00442-016-3647-9, 2016.

446 Schaller, J., Turner, B. L., Weissflog, A., Pino, D., Bielnicka, A. W., Engelbrecht, B. M. J.: Silicon in tropical

447 forests: large variation across soils and leaves suggests ecological significance, Biogeochemistry, 140, 161-

448 174, https://doi.org/10.1007/s10533-018-0483-5, 2018.

449 Schoelynck, J., Bal, K., Backx, H., Okruszko, T., Meire, P., and Struyf, E.: Silica uptake in aquatic and wetland

450 macrophytes: a strategic choice between silica, lignin and cellulose?, New Phytol., 186, 385–391,

451 https://doi.org/10.2307/27797561, 2010.

452 Schoelynck, J., Müller, F., Vandevenne, F., Bal, K, Barão, L., Smis, A., Opdekamp, W., Meire, P., and Struyf,

453 E.: Silicon-vegetation interaction in multiple ecosystems: a review, J. Veg. Sci., 25, 301–313,

454 https://doi.org/ 10.1111/jvs.12055, 2014.

455 Schoelynck, J., Subalusky, A. L., Struyf, E., Dutton, C. L., Unzué-Belmonte, D., Van de Vijver, B., Post, D. M.,

456 Rosi, E. J., Meire, P., and Frings, P.: Hippos (*Hippopotamus amphibius*): The animal silicon pump, Science

457 advances, 5(5), p.eaav0395, https://doi.org/10.1126/sciadv.aav0395, 2019.

458 Schuldt, A., Ebeling, A., Kunz, M., Staab, M., Guimarães-Steinicke, C., Bachmann, D., Buchmann, N., Durka,

459 W., Fichtner, A., Fornoff, F., Härdtle, W., Hertzog, L. R., Klein, A.-M., Weisser, W., Wirth, C., Zhang, J.,

460 Bruelheide, H., and Eisenhauer, N.: Multiple plant diversity components drive consumer communities

461 across ecosystems, Nature Communications, 10, https://doi.org/10.1038/s41467-019-09448-8, 2019.

462 Soininen, E. M., Bråthen, K. A., Jusdado, J. G. H., Reidinger, S., and Hartley, S. E.: More than herbivory:

463 levels of silica-based defences in grasses vary with plant species, genotype and location, Oikos, 122, 30-

464 41, https://doi.org/10.1111/j.1600-0706.2012.20689.x, 2013.

465 Street-Perrott, F. A and, Barker, P. A.: Biogenic silica: a neglected component of the coupled global

466 continental biogeochemical cycles of carbon and silicon, Earth Surf. Proc. Land., 33, 1436–1457,

467 https://doi-org.ludwig.lub.lu.se/10.1002/esp.1712, 2008.

468 Strömberg, C. A. E., Di Stilio, V. S., and Song, Z.: Functions of phytoliths in vascular plants: an evolutionary

469 perspective, Funct. Ecol., 30, 1286–1297, https://doi.org/10.1111/1365-2435.12692, 2016.

470 Struyf, E. and Conley, D.: Emerging understanding of the ecosystem silica filter, Biogeochemistry, 107, 9–

471 18, https://doi.org/10.1007/s10533-011-9590-2, 2012.

472 Struyf, E., Smis, A., Van Damme, S., Garnier, J., Govers, G., Van Wesemael, B., Conley, D. J., Batelaan, O.,

473 Frot, E., Clymans, W., Vandevenne, F., Lancelot, C, Goos, P., and Meire, P.: Historical land use change has

474 lowered   terrestrial   silica   mobilization,   Nature   Communications,   1,   129,   https://doi.org/

475 10.1038/ncomms1128, 2010.

476 Tréguer, P. J. and De La Rocha, C. L.: The World Ocean Silica Cycle, Annu. Rev. Mar. Sci., 5, 477–501,

477 https://doi.org/10.1146/annurev-marine-121211-172346, 2013.

478 Tréguer, P., Nelson, D. M., Bennekom, A. J. V., DeMaster, D. J., Leynaert, A., Quéguiner, B.: The silica

479 balance   in   the   world   ocean: a   reestimate,   Science,   268,   375–379,

480 https://doi.org/10.1126/science.268.5209.375, 1995.

481   Van der Putten, W. H., Bardgett, R. D., Bever, J. D., Bezemer, T. M., Casper, B. B., Fukami, T., Kardol, P.,

482   Klironomos, J. N., Kulmatiski, A., Schweitzer, J. A., Suding, K. N., Van de Voorde, T. F. J., and Wardle, D. A.:

483   Plant-soil feedbacks: the past, the present and future challenges, J. Ecol., 101, 265–276,

484   https://doi.org/10.1111/1365-2745.12054, 2013.

485   van Eck NJ, Waltman L.: VOSviewer manual. Version 1.6.8, Centre for Science and Technology Studies,

486   Leiden,   NL: Leiden   University.

487   https://www.vosviewer.com/documentation/Manual_VOSviewer_1.6.8.pdf, 2018.

488   Vandevenne, F., Barão, A. L., Schoelynck, J., Smis, A., Ryken, N., Van Damme, S., Meire, P., and Struyf, E.:

489   Grazers: biocatalysts   of   terrestrial   silica   cycling,   Proc.   Biol.   Sci.,   280,   20132083,

490   https://doi.org/10.1098/rspb.2013.2083, 2013.

491   Vandevenne, F., Struyf, E., Clymans, W., and Meire, P.: Agricultural silica harvest: have humans created a

492   new loop in the global silica cycle?, Front. Ecol. Environ., 10, 243–248, https://doi.org/10.1890/110046,

493   2012.

494   Vitousek, P. M.: Nutrient Cycling and Limitation: Hawai'i as a Model System, Princeton University Press,

495   Princeton, https://doi.org/ 10.1111/j.1442-9993.2005.01458.x, 2004.

496   Vivancos, J., Labbé, C., Menzies, J. G., Bélanger, R. R.: Silicon-mediated resistance of Arabidopsis against

497   powdery mildew involves mechanisms other than the salicylic acid (SA)-dependent defence pathway, Mol.

498   Plant Pathol., 16, 572–582, https://doi.org/10.1111/mpp.12213, 2015.

Tables and Figures

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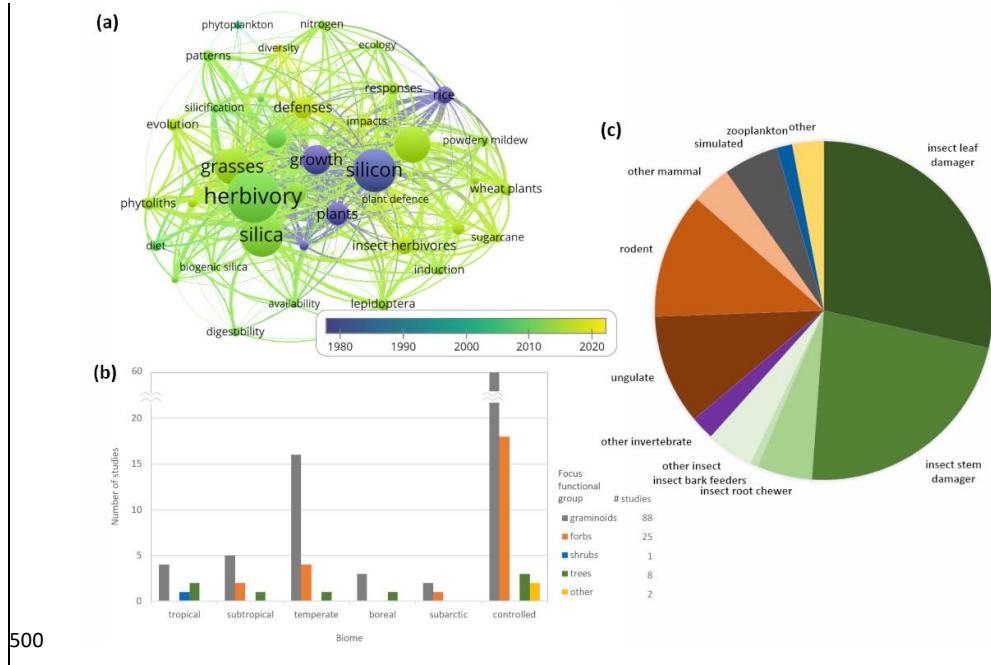
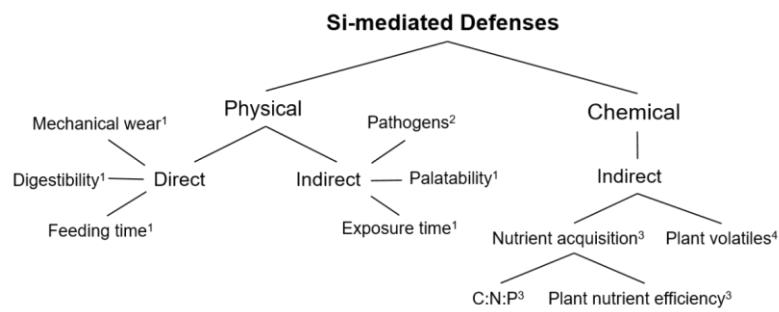


Figure 1 Summary of literature review. **(a)** Network map of keywords from publications between 1900-2020 in the Web of Science core collection database generated using search terms "silic*" and "herbivor*" and not "in silico" (314 results). Bubble and word size is scaled to the total occurrence of the keywords in all publications (only > 10 occurrences displayed), more proximate bubbles/keywords co-occur more often in the publications surveyed. The year indicates the average publication year of the documents in which a keyword occurs. The map was created with VOSviewer software (van Eck and Waltman 2018). **(b)** Number of publications investigating each plant functional type and biome using the three search terms. We filtered the 314 results until only those publications that directly studied Si and herbivory remained (119 publications). **(c)** Percentage distribution of herbivore types for all 119 studies that directly investigated

510 silicon and herbivory. The list of data sources and classifications for Fig. 1 are archived at doi:

511 10.6084/m9.figshare.12026997.

512

513 **Figure 2** Direct and indirect physical and chemical plant Si-mediated defenses to herbivory .[1]Massey et al.,

514 2009 and references therein; [2]Lev-Yadun and Halpern, 2019; [3]Neu et al., 2017; [4]Liu et al., 2017.

515 **Table 1** Estimated Si fluxes by atmosphere, mineral weathering and herbivory by major terrestrial habitat

516 type. ANPP is aboveground net primary productivity. [1]Cebrian, 2004; [2]Hodson et al., 2005; [3]as calculated

517 by Carey and Fulweiler 2012; [4]Street-Parrott and Barker, 2008 and references therein; [5]modeled by

518 Ribeiro et al., 2019; [6]Ariyanto et al., 2019.

Habitat type[1]	Herbivory[1] (% ANPP)	ANPP[1] (g C m^{-2} y^{-1})	% Si by dry weight[2,3]	Si:C[3]	Herbivory (g Si m^{-2} y^{-1})	Atmospheric[4] (g Si m^{-2} y^{-1})	Weathering[4] (g Si m^{-2} y^{-1})
Tundra shrublands and grasslands	1.8 ± 0.6	95.3 ± 31.0	1.07	0.02	0.04	-	-
Temperate/tropical shrublands and forests	7.9 ± 1.5	334.6 ± 24.9	0.26	0.01	0.15	0.004 - 0.2	0.3-3.2
Temperate/tropical grasslands	34.1 ± 5.3	239.4 ± 34.0	1.33	0.03	2.31	0.2	0.4-2.5
Freshwater and marine marshes	16.8 ± 5.0	958.9 ± 179.0	0.62	0.01	2.13	-	-
Mangroves	3.5 ± 0.5	500[5]	0.43[6]	0.01	1.60	-	-

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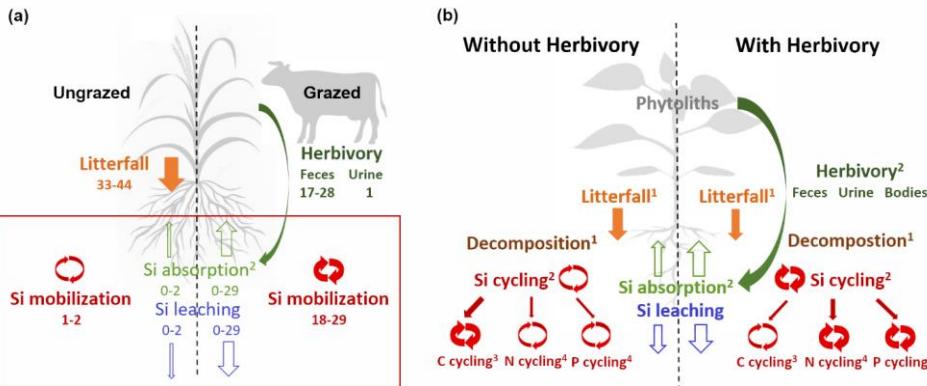
Figure 3 (a) Schematic of Si fluxes (kg ha^{-1} yr^{-1}) in hypothetical ungrazed and grazed grassland, dominated

by cows, adapted from Vandevenne et al., 2013. Annual net primary production is assumed to be the same

for both systems (11,000 kg ha^{-1} yr^{-1}) and all biomass is converted to litter or consumed by grazers in the

grazed system. A biomass conversion ratio of 1 : 4 for grass versus feces is suggested for all herbivores.

Mobilization percentages for faeces are based on ranges (minimum - maximum values) obtained in a

dissolution experiment by Vandevenne et al., 2013 after 24 h in rain water; for urine, a conservative

estimation of 3% mobilization was used. **(b)** Schematic of potential nutrient cycle differences in the plant-

soil system with and without herbivory. Size of arrows denotes the size of the flux relative to the

alternative scenario. [1]Schaller et al., 2016 [2]Brizuela et al., 1986; [3]Street-Perrott and Barker 2008; [4]Neu et

al., 2017; Schaller et al., 2017.