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1 Marschner Review

2 **Silicon dynamics through the lens of soil-plant-animal interactions:**  
3 **perspectives for agricultural practices**

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16  
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22 The authors declare that there is no conflict of interest.

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24 All data generated or analyzed during this study are included in this published article and its supplementary  
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39

40 **Abstract**

41 ***Background***

42 Silicon (Si) is increasingly recognized as a pivotal beneficial element for plants in ecology and  
43 agricultural sciences, but soil-plant Si cycling has been considered mostly through the prism of  
44 abiotic mineral weathering, whilst numerous biological processes have been overlooked.  
45 Leveraging ecological processes that impact soil-plant Si cycling in cropping systems might  
46 improve crop Si status, but this remains hypothetical to date.

47 ***Scope***

48 We aim to comprehensively compile information about biotic and abiotic processes driving soil-  
49 plant Si cycling, and translate their potential beneficial effects in agricultural practices. We  
50 emphasize the fundamental need to consider the effects of agricultural practices on Si mobility in  
51 soil-plant systems when striving towards sustainable agroecosystems.

52 ***Conclusions***

53 Regarding soil abiotic factors, degree of soil weathering, mineralogy, texture and pH are key  
54 predictors of soil Si dynamics, while soil aggregation processes deserve further investigation. The  
55 biological processes associated with mycorrhizal associations, silicate-solubilizing bacteria, and  
56 soil macrofauna enhance Si mobility in soil-plant systems, while the effect of root exudates is  
57 likely, but deserves further studies. Large herbivores strongly affect soil-plant Si mobility by  
58 increasing plant-derived Si turnover rates and redistribution, thereby making integrated crop-  
59 livestock systems a promising perspective to improve crop Si status. Recycling crop residues and  
60 implementing suitable cover crops promotes Si mobility in soil-plant systems by leveraging the  
61 relatively high solubility of plant-derived Si-bearing minerals. The soil-root-microorganism

62 interactions facilitated by cereal-legume intercropping systems also contributes to the mobility of  
63 Si in the soil-plant continuum. The capacity of certain agricultural practices to increase Si  
64 mobility in soil-plant systems stresses the need to understand complex soil-plant-animal  
65 interactions when aiming to enhance Si-based plant stress resistance in agroecosystems.

66 **Keywords:** large herbivores; cover crops; intercropping; integrated crop-livestock systems;  
67 nutrient-acquisition strategies; sustainable agroecosystems; recycling crop residues; facilitation;  
68 biochar

## 69 **Introduction**

70 Silicon (Si) is taken up by all vascular plants and contributes to a wide range of functions  
71 (Epstein 1994). It is deposited as hydrated amorphous silica in plant tissues ( $\text{SiO}_2 \cdot n\text{H}_2\text{O}$ ;  
72 phytoliths) and helps mitigate several plant biotic and abiotic stresses (Ma 2004; Liang et al.  
73 2007; Zhu and Gong 2014; Cooke and Leishman 2016; Hartley and DeGabriel 2016; Debona et  
74 al. 2017; Coskun et al. 2019), can be used as a cheap plant structural component (Raven 1983),  
75 and, eventually, increase plant primary productivity and crop yield (Savant et al. 1999; Liang et  
76 al. 2015b; Tubana et al. 2016; Xu et al. 2020). The essentiality of Si for plants remains debated  
77 and challenging to assess (Epstein 1994; Coskun et al. 2019), but overwhelming evidence show  
78 its importance for plant functioning. It is therefore increasingly considered a key element in plant  
79 ecology (Cooke and Leishman 2011; Katz 2019) and agriculture, especially considering the  
80 importance of Si-accumulating species in global food production (e.g., wheat, rice, sugarcane)  
81 (Fig. 1) (Meyer and Keeping 2000; Datnoff et al. 2001; Haynes 2014; Liang et al. 2015b; Tubana  
82 et al. 2016).

83 Over the last 30 years, soil scientists and biogeochemists studied Si in a wide range of  
84 environments to explore the role of soil properties and vegetation on soil-plant Si cycling (Bartoli  
85 1983; Alexandre et al. 1997; Lucas 2001; Derry et al. 2005; Sommer et al. 2006; Henriot et al.  
86 2008b, a; Cornelis et al. 2010; Haynes 2014; Cornelis and Delvaux 2016; Meunier et al. 2018;  
87 Vander Linden and Delvaux 2019; de Tombeur et al. 2020c, a, b; Schaller et al. 2021). The  
88 processes and factors governing Si release rates from minerals are well documented (Sommer et  
89 al. 2006; Churchman and Lowe 2012; Haynes 2014; Cornelis and Delvaux 2016; Schaller et al.  
90 2021), as are the influence of plant-induced mechanisms (bioweathering and Si uptake) on  
91 terrestrial Si cycling (Lucas et al. 1993; Alexandre et al. 1997; Street-Perrott and Barker 2008;  
92 Haynes 2017; de Tombeur et al. 2020a). However, how certain aspects of the soil-plant-animal  
93 continuum influence Si mobility in both natural systems and agroecosystems have been  
94 overlooked, especially the contribution of biotic factors. Yet, a detailed understanding of soil-  
95 plant-animal interactions influencing Si dynamics is paramount if we seek to benefit from Si-  
96 related plant functioning in agriculture (Acevedo et al. 2021).

97 Despite its ubiquity in soils (2<sup>nd</sup> most abundant element of the Earth's crust ; Wedepohl 1995),  
98 long-term mineral weathering and subsequent desilication (i.e. Si loss by leaching) result in soils  
99 with low plant-available Si concentrations in many areas of the world (approximately 3500  
100 million hectares, as estimated by the land area supporting desilicated soils: Ferralsol, Podzol,  
101 Arenosol, Lixisol, Plinthosol, Acrisol and Alisol; WRB 2015), particularly in tropical and  
102 subtropical regions where soils tend to be older and leaching intensity greater (Savant et al.  
103 1999). In addition, agriculture further enhances desilication by harvesting and exporting large  
104 amount of Si (Desplanques et al. 2006; Struyf et al. 2010; Clymans et al. 2011; Guntzer et al.

105 2012; Keller et al. 2012; Vandevenne et al. 2015; Carey and Fulweiler 2016; Tubana et al. 2016;  
106 Vander Linden and Delvaux 2019). These days, rock-derived Si fertilizers are routinely applied  
107 in some agroecosystems to counterbalance these detrimental effects (Savant et al. 1999; Datnoff  
108 et al. 2001; Haynes 2014; Liang et al. 2015b), and intensifying this practice might even be  
109 beneficial in less-weathered and desilicated environments (Tubana et al. 2016). However, such a  
110 practice relies on non-renewable resources, and low accessibility to common, rock-derived Si  
111 fertilizers in some tropical regions can jeopardize the Si benefits in these sensitive  
112 agroecosystems. Harnessing ecological processes that increase soil-plant Si mobility by  
113 promoting specific agricultural practices may improve the Si status of crops worldwide, while  
114 decreasing the need for non-renewable mineral fertilizers (Lambers et al. 2011; Richardson et al.  
115 2011; Mariotte et al. 2018). Indeed, recent evidence demonstrates the positive impact of certain  
116 agricultural practices such as intercropping, cover crops or integrated crop-livestock systems, on  
117 nutrient management, especially for phosphorus (P) (Hallama et al. 2019; Tang et al. 2020;  
118 Carlos et al. 2020).

119 In this review, we aim to compile knowledge about biotic and abiotic factors that govern Si  
120 mobility in soil-plant systems and translate their potential benefits in agricultural practices. We  
121 specifically emphasize how overlooked ecological/biological processes are pivotal when favoring  
122 Si biocycling in agroecosystems, and advocate the permanent need to nurture our understanding  
123 of complex interactions between physico-chemical and biological soil processes to develop  
124 sustainable agroecosystems.

125 **Biotic and abiotic factors affecting soil-plant Si cycling**

126 *Physico-chemical processes controlling soil Si dynamics*

127 Over the past decade, many studies reported an increase in plant-available Si concentrations with  
128 increasing soil pH when multiple soils were considered together (Phonde et al. 2014; Miles et al.  
129 2014; Puppe et al. 2015; Klotzbücher et al. 2018b; Meunier et al. 2018; Schaller et al. 2018,  
130 2021; Haynes 2019; Caubet et al. 2020; de Tombeur et al. 2020b). Prolonged soil acidification  
131 during pedogenesis is associated with the loss of reactive Si-bearing minerals (through mineral  
132 dissolution and subsequent lixiviation of dissolved Si) and increased desilication (Savant et al.  
133 1999; Chadwick and Chorover 2001; Sommer et al. 2006; Henriot et al. 2008a; Liang et al.  
134 2015a; de Tombeur et al. 2020b). Consequently, plant-available Si concentrations inevitably  
135 decrease with the relative enrichment of poorly weatherable minerals and the decrease in soil pH  
136 during pedogenesis (Savant et al. 1999; Liang et al. 2015a; Haynes 2019; de Tombeur et al.  
137 2020b). However, increasing soil pH is also associated to a decrease in plant-available Si  
138 concentrations, because Si adsorption onto the surface of oxides and silicates increases gradually  
139 to about pH 9.5, reflecting the  $\text{H}_4\text{SiO}_4/\text{H}_3\text{SiO}_4^-$  pKa of 9.47 (Jones and Handreck 1963;  
140 McKeague and Cline 1963; Beckwith and Reeve 1964; Hingston and Raupach 1967; Hingston et  
141 al. 1972; Obihara and Russell 1972; Philippini et al. 2006; Nguyen et al. 2017; Haynes and Zhou  
142 2018). This adsorption process is also dependent on condensation processes (Schaller et al. 2021)  
143 as adsorption of polysilicic acid is less reversible than monosilicic acid (Dietzel 2002). On the  
144 other hand, a high pH could also increase plant-available Si concentrations via increasing  
145 dissolution rates of aluminosilicates from soil pH 7.5/8 (Drever 1994; Kelly et al. 1998), together  
146 with increased phytolith dissolution rates with increasing soil pH from 3 to 10 (Frayse et al.  
147 2006b, 2009). Overall, although the controls of soil weathering, mineralogy and texture on plant-  
148 available Si are now well understood, especially for the silicate weathering domain (Cornelis and

149 Delvaux 2016; de Tombeur et al. 2020b), how high pH and carbonate minerals influence Si plant-  
150 availability remains unclear, because they are driven by antagonistic processes (Haynes 2019).

151 Beyond that, the complex physical organization of soil particles and accessibility to roots teach us  
152 how challenging it is to make the assessment of nutrient and Si availability accurate and  
153 reproducible. For instance, capturing the effect of condensation state of silicic acid on the  
154 measurements of plant-available Si by specific extractions (Schaller et al. 2021) is challenging. In  
155 particular, the relation between soil pH and mineralogy should be visited through the lens of  
156 polymerization and depolymerization processes influencing the equilibrium from monosilicic  
157 acid and polysilicic acid to amorphous silica precipitates over very short time scales (hours to  
158 days) (Dietzel 2000). Indeed, polymerization rates of monosilicic acid and its precipitation as  
159 amorphous silica increase strongly with increasing pH and ionic strength (Icopini et al. 2005). As  
160 suggested by Schaller et al. (2021), the activity of monosilicic acid in soil solution, which is  
161 directly related to plant-available Si concentrations, is largely dependent on solid-liquid  
162 equilibrium that vary on very short time scales (hours to days), because of daily and seasonal  
163 variations of water dynamics in soil porosity (Zabowski and Ugolini 1990). The short-term  
164 variations of water content are certainly a key driver of polymerization, complexation and  
165 adsorption reactions, which govern the availability of monosilicic acid for plants. The polymers  
166 of polysilicic acid and submicrometric colloids of amorphous silica precipitating in soil porosity  
167 could in turn influence the water holding capacity and aggregation, by clogging the porosity and  
168 cementing particles together (Schaller et al. 2021).

169 Despite a potential role of amorphous silica on soil aggregation (Schaller et al. 2021), how the  
170 interactions between soil mineral and organic constituents (Six et al. 2004) impact the extent to



171 which minerals can be dissolved in aggregates is not understood. In this regard, Li et al. (2020b)  
172 showed that soil microaggregates contribute over 60% of the total phytolith stock in a Retisol.  
173 The authors proposed that entrapment of phytoliths in aggregates might slow down their  
174 dissolution, and increase their persistence in soils and sediments. In addition, soil aggregates host  
175 *microbial hotspots* in pores or at mineral surfaces creating specific soil micro-environments  
176 where microbial processes are accelerated as compared to the average rates in the bulk soil, i.e.  
177 the *hot moments* (Kuzyakov and Blagodatskaya 2015). The bio-induced weathering processes in  
178 these hotspots most likely also impact soil Si release rates into the soil solution (Uroz et al. 2009),  
179 supporting the need to further investigate the role of soil aggregation on soil Si dynamics. This is  
180 of special interest since anthropogenic land transformations (e.g., tillage) substantially impact soil  
181 aggregation processes, affecting soil structure (Mikha and Rice 2004; Wright and Hons 2005;  
182 Fonte et al. 2014; Or et al. 2021).

183 Besides the role of soil solution chemistry on Si availability in the vicinity of roots, it is also  
184 recognized that Si compete with other ions via sorption/desorption mechanisms on soil  
185 exchangeable sites (Matychenkov and Ammosova 1996; Klotzbücher et al. 2020). In particular,  
186 research has long suggested competition between Si and phosphate ions (Smyth and Sanchez  
187 1980; Kundu et al. 1988; Matychenkov and Ammosova 1996; Owino-Gerroh and Gascho 2004;  
188 Konhauser et al. 2007; Reithmaier et al. 2017; Hilbrandt et al. 2019; Hömberg et al. 2020;  
189 Klotzbücher et al. 2020; Schaller et al. 2020). Such mechanism could explain the benefits of Si  
190 addition on plant P nutrition (Hall and Morison 1906; Fisher 1929; Singh and Sarkar 1992;  
191 Owino-Gerroh and Gascho 2004; Eneji et al. 2008; Neu et al. 2017), even though other  
192 mechanisms were postulated (Ma and Takahashi 1990a, b, 1991a; Kostic et al. 2017; Pavlovic et

193 al. 2021). In addition to P, Si may also compete with dissolved organic matter (Reithmaier et al.  
194 2017; Klotzbücher et al. 2020), selenium (Jordan et al. 2009), arsenic (Christl et al. 2012) and  
195 iron (Hömberg et al. 2020). Such sorption/desorption competitive mechanisms are pH-dependent,  
196 with rates decreasing with pH given the lower chemical reactivity of monosilicic acid at acidic  
197 conditions (Owino-Gerroh and Gascho 2004; Konhauser et al. 2007; Jordan et al. 2009; Christl et  
198 al. 2012). It is therefore key to buffer the pH of the sorption/desorption isotherms because it is  
199 certainly influenced by the use of alkaline Si fertilizers (e.g., calcium silicates).

200 Overall, although the controls of soil weathering degree and mineralogy on soil Si dynamics are  
201 now well understood (Cornelis and Delvaux 2016), more attention should be given to the process  
202 of polymerizing silicic acid from monosilicic and polysilicic acid to amorphous silica precipitates  
203 (Schaller et al. 2021). Soil porosity, as well pore tortuosity and connectivity, should also be  
204 considered for their influence on monosilicic acid activity in soil solution, as should soil  
205 aggregation. Finally, while the size and type of minerals as well as the ionic composition of pore  
206 water together control dissolution kinetics, furthering how temporal variations of water content  
207 (hourly to seasonally changes) affect plant-available Si is certainly worthwhile goal. Getting  
208 closer to the actual plant-availability of Si will therefore require to reconcile microscale soil  
209 processes with the extractable solutions used to assess Si concentrations in soil solution.

### 310 ***Biological processes controlling soil Si dynamics***

#### 311 *Silicon biocycling: the high reactivity of phytoliths*

312 In addition to the weathering of rock-derived minerals, the dissolution of soil phytogenic silicates  
313 (phytoliths) also strongly impact Si dynamics (Bartoli 1983; Alexandre et al. 1997; Meunier et al.  
314 1999; Derry et al. 2005; Farmer et al. 2005; Sommer et al. 2013; de Tombeur et al. 2020a).

315 Biogeochemical mass-balance calculations have long reported that a significant fraction of Si in  
316 the soil solution is derived from the dissolution of the phytogenic Si pool (Bartoli 1983;  
317 Alexandre et al. 1997, 2011; Gérard et al. 2008), because of its high solubility compared with that  
318 of crystalline Si-bearing minerals (Frayse et al. 2006b, 2009; Cornelis and Delvaux 2016). This  
319 challenged the common view that plant-available Si concentrations were mainly driven by soil  
320 parent material, weathering degree, and subsequent soil mineralogy/texture (Savant et al. 1999;  
321 Chadwick and Chorover 2001; Henriot et al. 2008a, b; de Tombeur et al. 2020b). To reconcile the  
322 control of geochemical and biological processes on Si release in the soil solution, Cornelis and  
323 Delvaux (2016) suggested that the biological Si feedback loop (phytolith formation in plants and  
324 dissolution in soils) takes over soil litho/pedogenic pools in advanced soil weathering stages. This  
325 contention was recently supported by the use of long-term soil chronosequences where plant-  
326 available Si concentrations are mainly governed by soil-derived Si-bearing minerals (clay  
327 minerals) in early and intermediate stages of weathering (de Tombeur et al. 2020b), but  
328 increasingly by the recycling of phytoliths in old and highly-weathered soils dominated by  
329 poorly-soluble quartz minerals (de Tombeur et al. 2020a). The significant effect of vegetation on  
330 the soil-plant Si cycle explains why land-use changes and management affect the global Si cycle  
331 (Struyf et al. 2010; Clymans et al. 2011; Vandevenne et al. 2015; Carey and Fulweiler 2016).

332 Some soil organisms also accumulate Si to form various siliceous structures (Ehrlich et al. 2010;  
333 Puppe 2020). They are classified as zoogenic Si pool (e.g., sponge spicules that get into the soils  
334 mostly from freshwaters through aeolian transport or *in situ* production; Łukowiak 2020),  
335 bacterial Si (e.g., *Proteus mirabilis*, Lauwers and Heinen 1974), fungal Si, protozoic Si (e.g.,  
336 testate amoeba shells) or protophytic Si (e.g., diatom frustules) (Sommer et al. 2006; Ehrlich et

337 al. 2010; Puppe et al. 2015; Puppe 2020). Recent evidence suggest that these pools are of a  
338 similar magnitude as the phytogenic pool, and in turn influence the terrestrial Si cycle (Sommer  
339 et al. 2013; Puppe et al. 2014, 2015, 2016). In particular, annual biosilicification from testate  
340 amoebae ranges from 17 to 80 kg ha<sup>-1</sup> yr<sup>-1</sup> depending on soil and ecosystem properties which is  
341 similar to or even exceeds annual Si uptake by terrestrial vegetation (Sommer et al. 2013; Puppe  
342 et al. 2015; Vander Linden and Delvaux 2019). This pioneering work opened new perspectives  
343 on the role of Si-based life forms on soil-plant Si cycling (Puppe 2020).

#### 344 *Biological weathering of Si-bearing minerals*

345 In addition to the production of an easily weatherable Si pool, plants are extremely active when it  
346 comes to enhancing weathering ability of different soil constituents, either directly or indirectly.  
347 Nevertheless, plants are not stand-alone entities in their ability to affect Si cycling, but should be  
348 considered as “holobionts”, which includes the microbiome associated with their development  
349 (Vandenkoornhuysen et al. 2015). There are numerous well-known mechanisms by which the  
350 actors of the soil-plant continuum contribute to the dissolution of Si-bearing minerals and  
351 extensive reviews can be found elsewhere (Finlay et al. 2020; Dontsova et al. 2020). Briefly,  
352 these mechanisms can be divided into two categories: biochemical and biophysical weathering.  
353 These processes are not mutually independent; rather, they often play cumulative or synergistic  
354 roles.

355 The main biochemical effect on Si dissolution is the modification of the chemical conditions in  
356 the rhizosphere. This occurs through the release of organic acids, either as a by-product of  
357 cellular metabolism or as root exudates, plant excretion of H<sup>+</sup> in exchange for cationic nutrients,  
358 formation of carbonic acid (Golubev et al. 2005; Brantley 2008) through the release of CO<sub>2</sub> via

359 root respiration or organic matter mineralization, and the release of inorganic acids from redox  
360 reactions (e.g. sulfuric acid via pyrite oxidation). Proton-promoted dissolution is supplemented  
361 by ligand-promoted dissolution where organic acids, in addition to their pH altering ability, can  
362 act synergistically with strong chelators such as phytosiderophores or carboxylates to further  
363 enhance weathering of Si-bearing minerals by destabilizing mineral lattices through the binding  
364 of metal cations (Bennett et al. 2001; Buss et al. 2007; Pastore et al. 2020). Biophysical  
365 mechanisms include hyphal tunneling, or boring and other mechanisms of penetration by plant  
366 roots or fungi along mineral weakness points (Smits et al. 2005; van Schöll et al. 2008; Teodoro  
367 et al. 2019). This, in turn, increases substrate porosity and, therefore, increases the mineral  
368 surface exposed to chemical weathering agents (Pawlik et al. 2016; Gadd 2017). Finally, plants  
369 and associated microorganisms can also affect water movement and retention capacity through  
370 uptake and biofilms and therefore strongly influence water residence time and weathering  
371 patterns (Lucas 2001; Flemming and Wingender 2010).

372 While the biological impact on weathering is recognized, its contribution to the mobility of  
373 nutrients in natural and agricultural systems, including Si, remains poorly understood. In the  
374 following, we therefore aim to assess the effects of each biological agent on Si plant-availability.

375 **Root exudates** Plant roots secrete a wide range of exudates that mobilize poorly-available  
376 nutrients in the rhizosphere (Dakora and Phillips 2002; Lambers et al. 2006; Finlay et al. 2020).  
377 A long history of experimental studies has shown the increase of silicate dissolution by root  
378 exudates, through organic acids (Stillings et al. 1996; Drever and Stillings 1997; Cama and Ganor  
379 2006; Bray et al. 2015) or forest floor extracts (van Hees et al. 2002). Increasing dissolution of  
380 silicates or pedogenic oxides in the presence of siderophores was also demonstrated, whether

381 they are microbial (Liermann et al. 2000; Buss et al. 2007) or root-derived (Reichard et al. 2005).  
382 However, despite their importance for plant nutrient acquisition, the role of root exudates in  
383 mobilizing Si for plant uptake has been overlooked. Yet root-released carboxylates do increase  
384 the mobility of P, K, Fe, Al, Ca, P and numerous micronutrients (Gerke et al. 1994; Ström et al.  
385 2005; Wang et al. 2011; Houben and Sonnet 2012; Abrahão et al. 2014; Colombo et al. 2014;  
386 Kabas et al. 2017; Teodoro et al. 2019), and there could be similar effects on soil-plant Si  
387 mobility.

388 Early work by Hinsinger et al. (2001) has shown the impact of banana (*Musa paradisiaca*), maize  
389 (*Zea mays*), canola (*Brassica napus*), and white lupin (*Lupinus albus*) on the weathering of a  
390 basaltic rock. After 36 days of growth, the amount of Si released from basalt in the presence of  
391 hydroponically grown plants was increased two-fold compared with the abiotic control. More  
392 recently, Burghilea et al. (2015) and Zaharescu et al. (2019) showed that buffalo grass  
393 (*Bouteloua dactyloides*) grown on schist and rhyolite for 124 to 603 days, respectively, increased  
394 the mobility of Si compared with that of an abiotic control. Furthermore, Gattullo et al. (2016)  
395 showed that Fe-deprived barley (*Hordeum vulgare*) plants rapidly released more exudates into  
396 the rhizosphere to mobilize Fe from amorphous Fe oxides. Then, when the soil-plant contact was  
397 extended to 12 days, plants overcame Fe nutritional stress and the exudation of organic ligands  
398 mobilized Si from smectite (Gattullo et al. 2016). These results demonstrate that root exudates  
399 are primarily influenced by macro- or micronutrients limitation, but that co-solubilization of Si is  
400 very likely (de Tombeur et al. 2021b). In support of this claim, recent studies showed an increase  
401 in leaf Si concentrations with decreasing soil P concentrations and Si plant-availability along a  
402 long-term soil chronosequence (de Tombeur et al. 2020a, 2021c), particularly in old and highly-

403 weathered environments where carboxylate-releasing strategies are common (Lambers et al.  
404 2008; Zemunik et al. 2015). This result suggests a role for carboxylates in mobilizing soil Si from  
405 poorly-soluble forms for plant uptake, as it is the case for manganese (Mn) along the Jurien Bay  
406 chronosequence (Hayes et al. 2014; Lambers et al. 2015; de Tombeur et al. 2021b). Future  
407 research is required to elucidate to which extent Si is co-mobilized by different nutrient-  
408 acquisition strategies. In addition, future studies should test if root exudation patterns are directly  
409 influenced by low Si availability.

410 **Mycorrhizal associations** With nearly 90% of plants harbouring either arbuscular mycorrhizal  
411 (AM) or ectomycorrhizal fungi (EM) symbionts (Brundrett 2002; Smith and Read 2008),  
412 mycorrhizas exhibit strong control over major ecosystem processes including plant nutrient  
413 acquisition (Marschner and Dell 1994; Clark and Zeto 2000; Richardson et al. 2009),  
414 biogeochemical cycles (Högberg et al. 2001; van Hees et al. 2006), plant diversity and  
415 productivity (Van Der Heijden et al. 1998, 2008) and weathering potential (Leake and Read  
416 2017; Smits and Wallander 2017). Plants enable mycorrhizal fungal growth and activity by  
417 translocating various organic compounds (sugars, lipids) into the roots (Jiang et al. 2017; Rich et  
418 al. 2017). In exchange of plant photosynthates, fungi develop hyphal networks into the soil and  
419 enhance weathering processes for lithogenic nutrient acquisition (Van Breemen et al. 2000; van  
420 Schöll et al. 2006, 2008). In 1990, Kothari et al. provided the first evidence of Si mobilization by  
421 mycorrhizal fungi by showing an increase in maize (*Zea mays*) root Si concentrations after  
422 inoculation with an arbuscular mycorrhizal fungi (Kothari et al. 1990). Since then, other studies  
423 have shown that the presence of mycorrhizal fungi may significantly increase the Si  
424 concentrations of different species (maize, sugarcane, banana, chickpea, pigeon pea, soybean),

425 and in different plant organs (roots, leaves, stems) (Table 1) (Yost and Fox 1982; Clark and Zeto  
426 1996; Garg and Bhandari 2016; Oye Anda et al. 2016; Frew et al. 2017b, a, 2020; Garg and  
427 Singh 2018; Gbongue et al. 2019). Root Si concentrations are positively correlated with the  
428 degree of arbuscular mycorrhizal colonization, which reduces root herbivory (Frew et al. 2017a).  
429 Moreover, mycorrhizal colonization increases root Si concentrations, but uniquely for plants  
430 growing on soils with low concentrations of plant-available Si (Frew et al. 2017a). This pattern  
431 was confirmed by other studies where the effects of mycorrhizal fungi on plant Si concentrations  
432 were less important, or even absent, when Si was supplied to plants (Oye Anda et al. 2016; Frew  
433 et al. 2017b).

434 Even if the effects of mycorrhizas on plant Si concentration depend on initial Si availability in  
435 soil, these results reveal that root mycorrhizal colonization can be a significant driver of plant Si  
436 uptake and concentrations in plants, with a direct impact on herbivory. In some cases, plant Si  
437 concentrations have indeed more than doubled after inoculation with mycorrhizal fungi (Oye  
438 Anda et al. 2016). More broadly, although phylogenetic variation and the presence or absence of  
439 Si transporters remain the main explanations for variation in plant Si accumulation (Hodson et al.  
440 2005; Ma et al. 2006, 2007; Deshmukh and Bélanger 2016; Deshmukh et al. 2020), nutrient-  
441 acquisition strategies like mycorrhizal associations and root-released carboxylates could play a  
442 significant, but so far overlooked role. This is of special interest since both strategies increase  
443 with decreasing P availability (Abbott et al. 1984; Tang et al. 2001; Covacevich et al. 2007; He et  
444 al. 2020), and P-depleted soils are often also Si-depleted, due to high weathering degree.

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451 **Table 1** – Effect of arbuscular mycorrhizal fungi on plant silicon (Si) concentrations in a range of plant species. We  
 452 used WebPlotDigitizer to extract data published as figures (Rohatgi 2012).

Plant	Organ	AM fungi	Increase in plant [Si] (%)	Reference
Maize ( <i>Zea mays</i> )	Shoot	<i>Glomus</i> sp.	+3% to +66% for acid soils -28% to -6% for alkaline soils +78% to +252% of Si content (weight by plant) for acid soils -9% to +25% of Si content (weight by plant) for alkaline soils	Clark and Zeto (1996)
Chickpea ( <i>Cicer arietinum</i> )	Shoot	<i>Funneliformis mosseae</i>	+17-20%	Garg and Bhandari (2016)
Banana ( <i>Musa acuminata</i> )	Pseudostem	<i>Rhizophagus irregularis</i>	+149% without Si +88% with Si	Oye Anda et al. (2016)
Banana ( <i>Musa acuminata</i> )	Leaves	<i>Rhizophagus irregularis</i>	+84% without Si +70% with Si	Oye Anda et al. (2016)
Banana ( <i>Musa acuminata</i> )	Roots	<i>Rhizophagus irregularis</i>	+109% without Si +30% with Si	Oye Anda et al. (2016)
Sugarcane ( <i>Saccharum</i> spp. hybrid)	Roots	<i>Glomus</i> sp.	+50% to +102% without Si -4% to +22% with Si	Frew et al. (2017b)
Sugarcane ( <i>Saccharum</i> spp. hybrid)	Roots	<i>Glomus</i> sp.	+42% to +71% for the low Si soil +0% to +18% for the high Si soil (ns)	Frew et al. (2017a)
Sugarcane ( <i>Saccharum</i> spp. hybrid)	Leaves	<i>Glomus</i> sp.	-29% to -21% for the low Si soil (ns) -20% to -4% for the low Si soil (ns)	Frew et al. (2017a)
Pigeon pea ( <i>Cajanus cajan</i> )	Leaves	<i>Rhizophagus irregularis</i>	+10%	Garg and Singh (2018)
Banana ( <i>Musa acuminata</i> )	Roots	<i>Rhizophagus irregularis</i>	+30% (Si content; weight by plant)	Gbongue et al. (2019)
Banana ( <i>Musa acuminata</i> )	Leaves	<i>Rhizophagus irregularis</i>	+14% (Si content; weight by plant)	Gbongue et al. (2019)
Soybean ( <i>Glycine max</i> )	Leaves	Unknown	+28% to +208% (depending on P supply)	Yost and Fox (1982)

453 'ns' stands for "not significant"

454

455 **Bacteria** Bacteria may colonize mineral surfaces, initiate or accelerate weathering, and stimulate  
 456 plant growth (Jackson 1971; Bosecker 1997; Banfield et al. 1999; Bennett et al. 2001; Vessey  
 457 2003; Calvaruso et al. 2006; Uroz et al. 2009; Burghelea et al. 2015; Zaharescu et al. 2019;

458 Finlay et al. 2020; Pastore et al. 2020). Bacteria often associate with fungi in soil to form biofilms  
459 on substrate surfaces via excretion of extracellular polymeric substances (EPS) which causes very  
460 localized weathering “hotspots” (Flemming and Wingender 2010; Deveau et al. 2018; Guennoc  
461 et al. 2018; Finlay et al. 2020). The subsequent dissolution of lithogenic nutrients can therefore  
462 be used by all organisms of these hotspots including plants, making the soil-plant continuum a  
463 very effective biogeochemical engineer and enhancing overall plant nutrition. Increased rates of  
464 weathering and Si release in the presence of certain bacteria have been demonstrated for different  
465 mineralogical contents such as feldspar (Barker et al. 1998; Welch and Ullman 1999; Wang et al.  
466 2015), hornblende (Liermann et al. 2000), mica (Barker et al. 1998; Liu et al. 2006; Wang et al.  
467 2015), smectite (Dong et al. 2003; Kim et al. 2004), amorphous silica (diatoms and sponge)  
468 (Bidle and Azam 1999; Schröer et al. 2003), granite (Song et al. 2007; Wu et al. 2008), basalt  
469 (Pastore et al. 2020), gneiss (Pastore et al. 2020) and saprolite (Brucker et al. 2020). These days,  
470 a large number of silicate-solubilizing bacteria (SSB) have been identified, belonging to different  
471 genera: *Aeromonas*, *Aminobacter*, *Azotobacter*, *Bacillus*, *Burkholderia*, *Cellvibrio*, *Collimonas*,  
472 *Dyella*, *Ensifer*, *Enterobacter*, *Flavobacterium*, *Frateuria*, *Janthinobacterium*, *Kosakonia*,  
473 *Labrys*, *Microbacterium*, *Paracoccus*, *Proteus*, *Pseudomonas*, *Rhizobium* and *Sphingomonas*  
474 (Uroz et al. 2009; Meena et al. 2014; Hu et al. 2018). Recently, Raturi et al. (2021) reviewed the  
475 role of SSB on the Si biogeochemical cycle and their role as potential biofertilizers.

476 In a pioneering work, Zahra et al. (1984) showed that soil inoculation with *Bacillus circulans*  
477 significantly increases Si release from different minerals and subsequent Si uptake by different  
478 crop species (barley, maize and clover), demonstrating a key role of bacteria in increasing plant-  
479 available Si. More recently, an increasing number of studies demonstrated the impact of SSB on

480 Si dissolution rates, plant Si uptake, and a potential positive effect on plant growth (Table 2 and  
 481 references therein). In these studies, soluble Si concentrations increased by up to 60%, while  
 482 plant Si content increased by up to 78% (Table 2). Besides the role of SSB in increasing silicates  
 483 dissolution, bacteria could also increase phytoliths dissolution and soluble Si through the  
 484 breaking down and mineralization of phytolith-occluded carbon (Hodson 2019). Future research  
 485 is needed to identify the abundance, diversity and functions of SSB in different geopedoclimatic  
 486 contexts, as well as their ability to stimulate soil-plant Si mobility.

487 **Table 2** – Effect of silicate-solubilizing bacteria on soluble/plant-available Si and leaf Si concentrations from the  
 488 literature. We used WebPlotDigitizer to extract data published as figures (Rohatgi 2012).

Plant	Organ	Bacteria	Increase in soluble [Si] (%)	Increase in plant [Si] (%)	Reference
Rice ( <i>Oryza sativa</i> )	Leaf	<i>Enterobacter ludwigii</i> GAK2	Not determined	+24%	Lee et al. (2019)
Rice ( <i>Oryza sativa</i> )	Leaf	<i>Rhizobium</i> sp. (IIRR-1)	from +12.4 to +60.2%, depending on silicates	from +9.0% to +78.5% of Si content (weight by plant), depending on silicates	Chandrakala et al. (2019)
Maize ( <i>Zea mays</i> )	Leaf and root	<i>Kosakonia</i> sp.	+10%	+23% for both leaf and root	Hu et al. (2019)
Rice ( <i>Oryza sativa</i> )	Leaf	<i>Bacillus amyloliquefaciens</i>	Not determined	+29%	Bist et al. (2020)
Rice ( <i>Oryza sativa</i> )	Whole plant	<i>Burkholderia eburnea</i> CS4-2	Not determined	+24%	Kang et al. (2017)
Maize ( <i>Zea mays</i> )	Leaf and root	<i>Flavobacterium</i> sp.	+16%	ns for leaves; +20% for roots	Hu et al. (2018)

489 'ns' stands for "not significant"

490  
 491 *Soil macrofauna*

492 Soil macrofauna like earthworms, beetles and termites contribute to nutrient cycling, soil  
 493 formation or primary production (Jouquet et al. 2011; Blouin et al. 2013), but little is known  
 494 about their effect on soil Si dynamics. Yet, soil macrofauna enhances the mineralization of  
 495 organic matter (Ingham et al. 1985; Schulmann and Tiunov, Alexei 1999), which might in turn  
 496 accelerate Si release in soil solution through enhanced phytoliths dissolution (Frayse et al.  
 497 2006a, 2010; Vandevenne et al. 2013). Macrofauna also increase the chemical (Jouquet et al.

498 2002; Carpenter et al. 2007) and physical (Suzuki et al. 2003) weathering of silicate minerals.  
499 Recently, Bitvutskii et al. (2016) showed that earthworm casts in a sandy and sandy loam soils  
500 had a significantly higher soluble Si concentration than the non-bioturbed soil (up to 12 times for  
501 *Lumbricus terrestris* casts in the sandy soil). Moreover, the concentrations and translocation rates  
502 of Si in the xylem sap of maize and cucumber plants significantly increased when plants grew on  
503 a soil previously bioturbed by earthworms. Following this research, Hu et al. (2018) isolated SSB  
504 from the gut of *Pheretima guillelmi*, and showed that they markedly increased the release of Si  
505 from feldspar and quartz powder, enhanced the uptake and accumulation of Si by maize, and  
506 promoted seedling growth. In addition, significantly more SSB were found in the earthworm gut  
507 than in the surrounding soil. The authors thus demonstrated that the increased soil-to-plant  
508 translocation of Si following earthworm activity was at least in part explained by the presence of  
509 SSB in earthworm guts (Hu et al. 2018). In accordance with this, Georgiadis et al. (2019) showed  
510 that the release of dissolved Si from quartz, which is highly resistant to weathering (Goldich  
511 1938), was much greater after passage through the gut of *Eisenia andrei*. They discussed this as  
512 resulting from a combination of mechanical alteration (Suzuki et al. 2003), and the presence of  
513 SSB in the earthworm gut (Hu et al. 2018). In addition, soil macrofauna strongly impact the  
514 redistribution of material in the soil profile (Jouquet et al. 2011; Blouin et al. 2013). For instance,  
515 Jouquet et al. (2020) showed that termite activity impacted the distribution of phytoliths and clay  
516 minerals type (1:1 versus 2:1) in south Indian forest soils which could, in turn, impact the  
517 concentration of plant-available Si in soil profiles. Overall, soil macrofauna have a significant but  
518 overlooked effect on soil Si dynamics, whose magnitude still needs to be determined.

519 *Large herbivores*

520 Large herbivores can cause important changes in ecosystem-scale nutrient cycling (Bardgett and  
521 Wardle 2003; Veldhuis et al. 2018; Forbes et al. 2019; Hwang and Metcalfe 2021). They can  
522 either accelerate nutrient cycling through the conversion of aboveground biomass into labile  
523 waste products, or decrease it through selective foraging and subsequent shifts towards species  
524 that decompose more slowly (Bardgett and Wardle 2003; Forbes et al. 2019). Compared with N,  
525 P and C (e.g., Veldhuis et al. 2018; le Roux et al. 2020; Sitters et al. 2020), the impact of large  
526 herbivores on Si dynamics is poorly quantified. Yet faeces of large herbivores exhibit high silica  
527 concentrations (from 17 to 163 g silica kg<sup>-1</sup> for large African herbivores ; Hummel et al. 2011), as  
528 does sheep urine (up to 259 mg silica L<sup>-1</sup> ; Nottle and Armstrong 1966). As a consequence, large  
529 herbivores strongly impact the land-to-ocean Si transfer by foraging grasses and transporting  
530 phytoliths from land ecosystems directly to rivers (Schoelynck et al. 2019). For instance, hippos  
531 of south-western Kenya contribute to 32% to the biogenic Si flux and more than 76% to the total  
532 Si flux to watercourses (Schoelynck et al. 2019). Given the abundance of Si-accumulating species  
533 in grassland ecosystems, the impact of large herbivores on phytolith redistribution within the  
534 same ecosystem (not land-to-river transfer; Schoelynck et al. 2019) is probably also significant.  
535 We estimate that large herbivores in a savanna ecosystem ingest and displace from  $0.005 \pm 0.002$   
536 kg Si ha<sup>-1</sup> yr<sup>-1</sup> (grey duiker) to  $23.2 \pm 3.8$  kg Si ha<sup>-1</sup> yr<sup>-1</sup> (buffalo) (Table 3). The higher value  
537 corresponds to yearly litterfall of a short grass ecosystem of the Central Great Plains, USA  
538 (Blecker et al. 2006). This redistribution of phytoliths could, in turn, modify the spatial variability  
539 of plant-available Si given their high reactivity in soil environments (Alexandre et al. 1997;  
540 Blecker et al. 2006; Sommer et al. 2013; de Tombeur et al. 2020a).

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544 **Table 3** – Estimation of yearly silicon (Si) inputs into soil by large herbivores in a savanna ecosystem, and their  
 545 potential effect on Si cycling.

Species	Scientific name	Dung produced <sup>a</sup> g ha <sup>-1</sup> day <sup>-1</sup>	Dung [BSi] <sup>b</sup> g kg <sup>-1</sup>	Dung Si input <sup>c</sup> kg Si ha <sup>-1</sup> yr <sup>-1</sup>	MRT <sub>particle</sub> <sup>d</sup> hours	Effect on Si cycling <sup>e</sup>
Buffalo (ruminant)	<i>Syncerus caffer</i>	1018	134 ± 22	23.2 ± 3.8	49	+++
Elephant	<i>Loxodonta Africana</i>	432	53 ± 11	3.9 ± 0.8	30	++
Grey duiker (ruminant)	<i>Giraffa camelopardalis</i>	1.3	22 ± 9	0.0 ± 0.0	45	+/-
Impala (ruminant)	<i>Aepyceros melampus</i>	200	123 ± 49	4.2 ± 1.7	-	++
Nyala (ruminant)	<i>Tragelaphus angasii</i>	8.6	38 ± 13	0.1 ± 0.0	-	+/-
White rhino	<i>Ceratotherium simum</i>	124	75 ± 13	1.6 ± 0.3	44	+
Wildebeest (ruminant)	<i>Connochaetes taurinus</i>	53	135 ± 15	1.2 ± 0.1	-	+
Zebra	<i>Equus burchellii</i>	77	126 ± 18	1.6 ± 0.2	28	+

546 <sup>a</sup>Data from Veldhuis et al. (2018)547 <sup>b</sup>Data from Hummel et al. (2011). Means of wet and dry season data were considered.548 <sup>c</sup>BSi was converted to Si by dividing by 2.14.549 <sup>d</sup>'Food particles' mean retention time (MRT) comes from Steuer et al. (2011) for Buffalo, Elephant, and Zebra, and from Müller et al. (2011) for  
550 Grey duiker and White rhino551 <sup>e</sup>Estimated through the combination of yearly dung Si input and MRT<sub>particle</sub> control on phytolith turnover rates (Vandevenne et al. 2013).

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553

554 Although silica ingestion can reduce the apparent digestibility of herbage (Shewmaker et al.  
 555 1989; Hartley and DeGabriel 2016; Johnson et al. 2021), how phytoliths are processed during  
 556 digestion remains poorly known. Some herbivores have a neutral to slightly alkaline stomach  
 557 (e.g., pH 7.3 for *Lama guanicoe* ; Beasley et al. 2015) and phytolith dissolution rates increase  
 558 significantly from pH 5 to pH 8 (Frayse et al. 2009). In 1971, Blackman & Bailey showed that  
 559 up to 39% of silica was dissolved after 24 h of ingestion in a cow rumen (Blackman and Bailey  
 560 1971). More recently, Vandevenne et al. (2013) showed that phytolith concentrations in cow,  
 561 sheep, horse and donkey faeces were two to four times higher than those in the plants prior to  
 562 ingestion and from which the faeces were derived. They also showed that readily-soluble Si  
 563 concentrations increased in faeces compared with pasture forage (except for horse faeces).  
 564 Moreover, relative to the initial phytolith content in dungs, 60%, 16% and 8% of Si was  
 565 mobilized in rain water after 24 h for cow, horse and sheep faeces, respectively, but only 4% for

566 the corresponding pasture forage. These results demonstrate that herbivores have a strong  
567 potential to increase Si mobility in soil-plant systems by releasing dissolved Si in urine and  
568 increasing phytolith turnover rates, probably through the degradation of plant tissues and an onset  
569 of phytolith dissolution in the digestive tract (Vandevenne et al. 2013).

570 Vandevenne et al. (2013) suggested that ruminants (sheep and cows), which achieve greater  
571 particle size reduction through higher food particles' mean retention time (MRT) (Johnson et al.  
572 2021), have a greater potential to quickly mobilize the highly-soluble fraction of phytoliths,  
573 partly via urine, compared to non-ruminants (horse and donkey). Following this idea, ruminants  
574 (that have longer food particles' MRT), such as buffalo or duiker, would increase the phytoliths  
575 turnover more strongly than non-ruminants such as elephant or zebra do (Table 3). Therefore,  
576 ruminants that produce large amounts of dung – which largely depends on body mass (Veldhuis  
577 et al. 2018) – will have a greater impact on soil-plant Si dynamics, and eventually on land-to-  
578 ocean Si transfer (Vandevenne et al. 2013), compared with non-ruminants that produce moderate  
579 amounts of dung (Table 3). Overall, large herbivores play a significant but overlooked role in Si  
580 biogeochemistry (but see Hwang and Metcalfe 2021) by affecting phytolith turnover rates and  
581 distribution in terrestrial ecosystems.

## 582 **Silicon and agricultural practices**

583 Knowledge acquired from complex natural systems can be used to increase the resource-use  
584 efficiency and productivity of modern agroecosystems (Lambers et al. 2011; Mariotte et al.  
585 2018). After highlighting biotic and abiotic factors influencing soil-plant Si mobility (Fig. 2),  
586 next we discuss the potential of certain agricultural practices to impact soil Si dynamics and  
587 stimulate soil-plant Si cycling.

588

589 ***Leveraging the high reactivity of phytoliths: recycling crop residues***

590 Recycling agricultural residues such as leaves, stems or grain husks is key to improve the crop Si  
591 status and limit long-term desilication (Guntzer et al. 2012; Meharg and Meharg 2015; Haynes  
592 2017; Puppe et al. 2021). Annual Si uptake by crop species may be an order of magnitude higher  
593 than that in natural ecosystems (Vander Linden and Delvaux 2019) and removing crop residues at  
594 harvest is common in some parts of the world (Klotzbücher et al. 2015) which lowers the soil  
595 phytolith pool (Desplanques et al. 2006; Guntzer et al. 2012; Keller et al. 2012).

596 The application of different crop residues to soil increases Na<sub>2</sub>CO<sub>3</sub>-extractable Si (up to 37% in  
597 Yang et al. 2020), water-soluble Si concentrations (up to 15% in Ma and Takahashi 1991b; up to  
598 50% in Watanabe et al. 2017; up to 44% in Yang et al. 2020), plant Si concentration (up to 17%  
599 in Ma and Takahashi 1991b; up to 136% in Sistani et al. 1997; up to 168% in Hossain et al. 2001;  
600 up to 57% in Yang et al. 2020), and plant Si uptake (up to 25% in Ma and Takahashi 1991b; up to  
601 212% in Marxen et al. 2016). The same pattern occurs for manure, which increases acetic acid-  
602 extractable Si and NaOH-extractable Si concentrations by 101% and 32%, respectively, after 10  
603 years of application to a Gleysol (Song et al. 2014). Klotzbücher et al. (2018b) also found that  
604 manure application tends to increase acetate-extractable Si concentrations, especially together  
605 with liming. These results highlight the benefit of returning phytoliths to topsoil because of their  
606 fast dissolution rates to replenish the soil solution in dissolved Si (Wickramasinghe and Rowell  
607 2006; Seyfferth et al. 2013; Marxen et al. 2016; Klotzbücher et al. 2018a; Puppe et al. 2021),  
608 with subsequent positive impacts on plant Si uptake. On the other hand, returning carbon-rich



609 phytoliths to topsoil could also possibly contribute to C sequestration, even though many  
610 questions about the phytoliths ability to sequester C on the long-term remain (Hodson 2019).  
611 Recently, the use of pyrolyzed Si-rich crop residues (i.e. Si-rich biochar) as a potential alternative  
612 to common Si fertilizers has attracted a lot of attention (Xiao et al. 2014; Li and Delvaux 2019;  
613 Wang et al. 2019b for reviews). According to Li and Delvaux (2019), the pyrolysis has the  
614 advantage of (1) concentrating Si in biochar compared with unpyrolyzed crop residues; (2)  
615 providing the same effect as liming and (3) enhancing the reactive surface area; both (2) and (3)  
616 contribute to increasing phytolith dissolution. Numerous recent studies show that the application  
617 of different biochars increases soil soluble Si and/or plant Si concentrations (Houben et al. 2014;  
618 Liu et al. 2014; Ibrahim et al. 2016; Qian et al. 2016; Koyama and Hayashi 2017; Abbas et al.  
619 2017; Alvarez-Campos et al. 2018; Li et al. 2018; Limmer et al. 2018; Leksungnoen et al. 2019;  
620 Li et al. 2019; Seleiman et al. 2019; Wang et al. 2019a; Huang et al. 2020; Wang et al. 2020; de  
621 Tombeur et al. 2021a), confirming its potential as a suitable Si fertilizer (Li and Delvaux 2019).  
622 The types of biochar used, application rates (on a Si basis), and increase in percentages of soil  
623 soluble Si and/or plant Si concentrations are reported in Table S1.

624 Recycling crop residues via direct incorporation, burning or biochar/manure/compost production  
625 and subsequent application has therefore a strong potential to increase crop Si uptake. However,  
626 the application rates used in most studies largely exceed coherent annual crop yields. For  
627 instance, considering biochar, the application of pyrolyzed material to concentrations of 1%  
628 (w/w) or more (bulk density of  $1.3 \text{ g cm}^{-3}$ ; depth incorporation of 10 cm), which corresponds to  
629 yearly crop yields of approximately  $43 \text{ t ha}^{-1}$  (taking into account a pyrolysis yield of 30%) is  
630 common. This generally exceeds mean cereal yields worldwide (up to about  $13 \text{ t ha}^{-1}$ ; Ritchie and

631 Roser 2013), except for sugarcane (up to about 120 t ha<sup>-1</sup>; Ritchie and Roser 2013), and the  
632 fraction not available for pyrolysis has to be considered. Li and Delvaux (2019) calculated that a  
633 realistic application rate of biochar in the tropics would be around 1.7 t ha<sup>-1</sup> yr<sup>-1</sup>, which is about  
634 an order of magnitude lower than what was applied in some studies. We, therefore, stress the  
635 importance of performing long-term studies in agroecosystems with minimal inputs from external  
636 sources and outputs of crop residues (Hughes et al. 2020), to better assess the long-term  
637 sustainability of such recycling practices. In these systems, detailed analyses of soil and plant Si  
638 pools must be conducted, as well as mass-balance calculations, to study the magnitude of  
639 desilication as a function of crop residue management. For example, Hughes et al. (2020)  
640 recently showed that enhanced Si accumulation in rice grain (including husks) in highly-  
641 weathered soil environments could further contribute to long-term desilication. Furthermore, the  
642 effect of crop residue quality on organic matter decomposition rates in contrasting soil, climatic  
643 and agricultural contexts should be considered because of its key role in dissolved Si release rates  
644 (Frayse et al. 2006a, 2010; Marxen et al. 2016; Nakamura et al. 2020).

#### 645 *Harnessing Si biocycling and recycling using cover crops*

646 Cover crops are grown specifically for covering the soil during the off-season to reduce soil  
647 erosion, increase soil organic matter content and microbial diversity, and improve nutrient  
648 cycling (Reeves 1994; Adetunji et al. 2020). The positive impact of cover crops on N, P and C  
649 cycles has been extensively demonstrated (Abdalla et al. 2019; Hallama et al. 2019), while their  
650 effects on soil Si dynamics for different cover crops species are unknown. In the short term,  
651 cover crops could have detrimental effects by consuming the pool of soil readily-soluble Si  
652 during the winter, lowering Si plant availability for main crops in summer. However, in the long

653 term, the yearly transfer of Si stored in the cover crop via plant residues will significantly  
654 increase the soil phytogenic Si pool, and the cover crop will reduce phytolith losses through  
655 erosion (Fig. 3a). This conversion of litho/pedogenic Si-bearing minerals to phytoliths could  
656 significantly stimulate Si mobility in agroecosystems since the dissolution rates of phytoliths are  
657 an order of magnitude greater than those of typical soil clay minerals (Frayse et al. 2009). Such  
658 positive effect would be particularly significant in highly-desilicated soils, where phytolith  
659 dissolution has a major effect on the soil-plant Si cycle (Alexandre et al. 1997; Sommer et al.  
660 2013; de Tombeur et al. 2020a).

661 Based on shoot biomass data of common cover crop species (Hallama et al. 2019), we estimated  
662 Si stocks in aboveground biomass of cover crops (Table 4). For legumes and *Brassica* sp. cover  
663 crops, from 2 to 56 kg Si ha<sup>-1</sup> could annually be brought to soil via crop residues. This range,  
664 despite being very large, approximately corresponds with the annual Si uptake in major forest  
665 ecosystems worldwide, except bamboo forests (Vander Linden and Delvaux 2019). The use of  
666 Poaceae sp. as cover crops would allow an extreme degree of annual Si inputs, up to 360 kg Si  
667 ha<sup>-1</sup> for *Lolium* sp., which approximately corresponds to Si uptake in sugarcane agroecosystems  
668 (Vander Linden and Delvaux 2019). In addition, cover crops may also impact Si dynamics by  
669 providing a legacy of increased mycorrhizal abundance, modifying rhizosphere physico-chemical  
670 properties (e.g., pH, soil aggregation, root exudates) or changing soil microbial communities and  
671 earthworms abundance (Roarty et al. 2017; Hallama et al. 2019; Adetunji et al. 2020; Euteneuer  
672 et al. 2020). Finally, Si-rich cover crops could diminish herbivore populations, with beneficial  
673 legacy effects on the main crop (Vernavá et al. 2004).

674

675

676

**Table 4** – Estimation of shoot Si stocks in common cover crop species.

	Family	Shoot biomass <sup>a</sup> (t ha <sup>-1</sup> )	Shoot Si concentration <sup>b</sup> (g kg <sup>-1</sup> )	Shoot Si stocks (kg ha <sup>-1</sup> )	
<b>Legume cover crops</b>					
677					
678					
679					
680	<i>Lupinus</i> sp.	Fabaceae	0.7-12.4 (n=6)	2.8-4.5	2-56
681	<i>Pisum sativum</i>	Fabaceae	3.7-3.9 (n=3)	2.8-5.6	10-22
682	<i>Vicia</i> sp.	Fabaceae	4.3-8.0 (n=7)	2.4-4.8	10-38
<b>Non-legume cover crops</b>					
683					
684	<i>Avena</i> sp.	Poaceae	7.9-13.2 (n=6)	11.5-15.1	91-200
685	<i>Lolium</i> sp.	Poaceae	1.4-10.0 (n=3)	9.7-36.4	14-364
686	<i>Secale cereale</i>	Poaceae	1.5-12.7 (n=11)	12.6	19-160
687	<i>Brassica</i> sp.	Brassicaceae	2.2-4.1(n=4)	2.3-11.2	5-46
688					

688

689 <sup>a</sup>Data from Hallama et al. (2019)690 <sup>b</sup>Data from Hodson et al. (2005) for all species. Additional data from Xiao et al. (2016) for *Pisum sativum*, Hasan et al. (2020) for *Vicia* sp.,  
691 Soratto et al. (2012) for *Avena* sp. and Song et al. (2009) for *Brassica* sp.

692

693 ***Facilitative interactions: cereal-legume intercropping systems***

694 Intercropping (Smith and McSorley 2000) has the potential to globally increase yields, reduce  
695 fertilizer inputs and save land (Martin-Guay et al. 2018; Li et al. 2020a), while increasing soil C  
696 and N content, improving mineral nutrition and reducing effects of pests (Hinsinger et al. 2011;  
697 Brooker et al. 2015; Cong et al. 2015; Xue et al. 2016; Tang et al. 2020). To our knowledge, the  
698 impact of intercropping systems on Si dynamics has been considered only once, through the  
699 study of rice (*Oryza sativa*) intercropped with water spinach (*Ipomoea aquatic*) (Ning et al.  
700 2017). Plant-available Si concentrations in soil were not markedly impacted by the intercropped  
701 system compared with rice monoculture, yet they significantly increased when water spinach was  
702 cultivated alone, likely because spinach accumulates less Si than rice (Ning et al. 2017).  
703 However, leaf Si concentrations and stocks (i.e. Si concentration × leaf dry weight) of rice plants  
704 significantly increased in the intercropping system compared with the rice monoculture (up to  
705 ~25% for Si concentrations and ~75% for Si stocks) (Ning et al. 2017). Moreover, the disease  
706 index of rice sheath and the incidence of leaf folders significantly decreased in the intercropped

707 system, which could be explained by (1) a role of physical barrier played by the strip distribution  
708 in intercropping system, (2) a more favorable field microclimate in the intercropping system, (3)  
709 the release of allelochemicals by water spinach, and/or (4) higher concentrations of silica-based  
710 defenses (Ning et al. 2017).

711 The pioneering work of Ning et al. has opened up new compelling directions in intercropping-Si  
712 research. Here, we propose different processes that could affect soil-plant Si dynamics in cereal-  
713 legume intercropping agroecosystems (Fig. 3b). First, more Si would be available for cereal crop  
714 uptake since grasses accumulate more Si than legumes. In the long term, cereal-legume  
715 intercropping might even slow down soil desilication, even though mass-balance calculations  
716 should be performed to estimate Si stocks in biomass and export from harvests. However, the  
717 opposite effect might occur for legume crops, for which less Si would be available than in a  
718 monoculture system (Ning et al. 2017). This is important to consider since Si has beneficial  
719 effects also for legumes, and may promote the symbiotic relationship with nitrogen-fixing  
720 bacteria in root nodules (Putra et al. 2020). Second, cereal-legume intercropping might induce a  
721 wide range of facilitative interactions (Li et al. 2014). Under conditions of Fe and Zn  
722 deficiencies, cereals such as wheat, barley, maize or rice secrete phytosiderophores in the soil  
723 solution that mobilize Fe and Zn (Ahmed and Holmström 2014), which can then be transferred to  
724 both crops (Zuo et al. 2000; Xue et al. 2016). The same mechanism applies to legumes that may  
725 secrete carboxylates to mobilize P, especially under P deficiency (Lambers et al. 2006, 2015;  
726 Pang et al. 2018), which could in turn benefit both crops (Xue et al. 2016; Lambers et al. 2018).  
727 As discussed above, Si co-solubilization or desorption by root exudates such as  
728 phytosiderophores and carboxylates is likely, but this needs to be further assessed to determine if

729 such facilitative interactions also occur for this element. Similarly, facilitation via common  
730 mycorrhizal networks and nutrient transfer can occur for N and P (Walder et al. 2012), but has  
731 not been addressed for Si. Third, earthworm abundance and biomass can greatly increase in  
732 cereal-legume intercropping systems compared with monocultures (Schmidt et al. 2001, 2003)  
733 which could increase plant-available Si concentrations and Si soil-plant mobility (Fig. 2). Finally,  
734 intercropping might also impact Si dynamics by changing soil microbial diversity and modifying  
735 the physico-chemical properties of the rhizosphere (Brooker et al. 2015), but the direction of  
736 these processes needs to be elucidated.

### 737 *Grazers as biocatalysts of Si cycling: crop-livestock systems*

738 Despite recent simplification and specialization of agricultural systems worldwide, integrated  
739 crop-livestock systems have been employed for millennia and remain the main agriculture model  
740 for over two thirds of global farmers, and represent about half of the world's food (Russelle et al.  
741 2007; Herrero et al. 2010; Lemaire et al. 2014). Integrated crop-livestock systems have the  
742 potential to improve carbon and nutrient cycling/use efficiency (Alves et al. 2019; Brewer and  
743 Gaudin 2020; Carlos et al. 2020). Based on the evidence of Si mobilization by large herbivores  
744 (Fig. 2), we suggest several benefits of integrated crop-livestock systems on soil-plant Si  
745 dynamics, based on a simple pasture/crop rotation (Fig. 3c). First, large ruminants strongly  
746 increase biogenic silica turnover rates (Blackman and Bailey 1971; Vandevenne et al. 2013). For  
747 instance, Vandevenne et al. (2013) estimated that a cow-based pasture mobilizes between 18 and  
748  $28 \text{ kg Si ha}^{-1} \text{ yr}^{-1}$ , against  $1.3\text{-}1.8 \text{ kg Si ha}^{-1} \text{ yr}^{-1}$  in ungrazed pastures. In the long term, greater Si  
749 mobilization potentially accelerates soil desilication through Si leaching (Vandevenne et al.  
750 2013). However, in the short term, it will most likely increase plant-available Si concentrations

751 for the subsequent crop, especially if soil texture-related leaching potential is low. Second,  
752 pasture/crop rotations will reduce long-term soil desilication because Si exports through crop  
753 harvest will occur only once every two years. Finally, integrating crops and livestock impacts  
754 numerous aspects of soil-plant systems such as soil aggregation, microbial community  
755 structure/biomass and annual net primary production (Brewer and Gaudin 2020), which could  
756 ultimately also affect the soil-plant Si cycle. Crop-livestock systems are promising to enhance Si  
757 mobility in soil-plant systems, particularly through the effects of ruminants on phytolith turnover,  
758 and therefore deserve further investigations, including the time scales of different processes.

### 759 *Liming and soil-plant Si dynamics: a gap between theory and practice*

760 The effect of liming on soil pH in agroecosystems may affect Si dynamics through antagonistic  
761 processes (Fig. 3d), as discussed above. Therefore, the liming effect is still unclear because it  
762 strongly depends on the initial pedological context in terms of soil pH, mineralogy, buffering  
763 capacity and phytolith content (Haynes 2019; Vander Linden and Delvaux 2019). Previous  
764 studies showed either an increase (Castro and Crusciol 2013; Klotzbücher et al. 2018b) or a  
765 decrease (Kostic et al. 2017; Keeping et al. 2017; Haynes and Zhou 2018) in soil Si availability  
766 with liming, while others found no significant effect (Mathews et al. 2009; Bhat et al. 2010).  
767 However, different extractants were used to estimate plant-available Si concentrations in these  
768 studies (e.g.,  $\text{CaCl}_2$ , acetic acid). In fact, liming is expected to increase the pool of adsorbed Si,  
769 often associated with acetate and acetic acid extractants, while decreasing the soluble Si pool,  
770 often associated with  $\text{CaCl}_2$  or water extractants (Sauer et al. 2006; Georgiadis et al. 2013).  
771 Haynes and Zhou (2018) confirmed this pattern by showing an increase of Si-acetic acid by about  
772 75-110% and a decrease of Si- $\text{CaCl}_2$  by about 25-35% for the pH range 5.0-6.5 in limed Podzol

773 and Gleysol. The authors also found a decrease of alkali-extractable Si, suggesting a loss of  
774 phytoliths following increasing dissolution rates (Haynes and Zhou 2018). More recently, Caubet  
775 et al. (2020) showed that French agricultural soils had higher Si-CaCl<sub>2</sub> concentrations than non-  
776 cultivated soils. The authors interpreted this difference as resulting from the pH increase after  
777 liming that could modify clay mineralogy (Cornu et al. 2012) and increase phytolith dissolution  
778 for soils with clay size mineral contents ranging between 5 and 32%. In their study, soils were  
779 classified by parent material types, where soils developed on sediments were separated into two  
780 groups: carbonated soils (>1% carbonates) and non-carbonated soils (<1% carbonates). In the  
781 non-carbonated group, Si-CaCl<sub>2</sub> also correlates with the 2- $\mu$ m fraction cation exchange capacity,  
782 used as a proxy of the nature of clay-size minerals. This supports a possible effect of clay  
783 mineralogy on Si availability that can be superimposed on the liming effect in cultivated land  
784 compared with non-cultivated land (forests, wetlands, pastures, parks). Indeed, soils with higher  
785 weatherable mineral reserves and subsequently higher Si availability are preferred for agriculture.  
786 As soil extractants are only proxies for plant-available Si concentrations (e.g., Wu et al. 2020),  
787 the liming effect on soil Si dynamics should be addressed by quantifying plant Si concentrations.  
788 Although some studies showed that liming had no significant effect on plant Si uptake (Bhat et al.  
789 2010; Castro and Crusciol 2013; Keeping et al. 2017), others found a marked decrease (Mathews  
790 et al. 2009; Tavakkoli et al. 2011). In particular, Mathews et al. (2009) noted a decrease in Si  
791 concentrations of *Pennisetum clandestinum* of about 30% with increasing calcium carbonate  
792 application, and in the pH range of 5.2-6.2. This study could highlight that raising soil pH above  
793 6.0 may reduce plant Si uptake, possibly because of increased Si adsorption and subsequent  
794 decline of Si plant-availability. In addition, raising pH will increase polymerization rates of



795 monosilicic acid and its precipitation as amorphous silica, which could also decrease Si plant-  
796 availability (Icopini et al. 2005; Schaller et al. 2021). Besides, phytolith dissolution rates strongly  
797 increase in this pH range (Frayse et al. 2009) which possibly enhances plant Si uptake (Guntzer  
798 et al. 2012), but the size of the phytogenic Si pool is low compared with the litho/pedogenic-Si  
799 pool (Alexandre et al. 1997, 2011; Sommer et al. 2013). Phytoliths can, therefore, not be the main  
800 factor of Si plant-availability and subsequent plant uptake in certain pedological contexts (Keller  
801 et al. 2021). Overall, the effect of liming on soil-plant Si dynamics is still unclear because  
802 numerous antagonistic processes occur on different time scales (Fig. 3d) (Haynes 2019; Vander  
803 Linden and Delvaux 2019).

#### 804 **Conclusions and perspectives**

805 Soil-plant Si cycling is mainly studied through the prism of abiotic mineral weathering or plant Si  
806 uptake followed by soil phytoliths dissolution (e.g., Bartoli 1983; Lucas et al. 1993; Alexandre et  
807 al. 1997; de Tombeur et al. 2020a), while biotic factors tend to be overlooked. Besides, numerous  
808 studies on biological weathering have been conducted, on different scales (Barker et al. 1998;  
809 Banfield et al. 1999; Lucas 2001; Uroz et al. 2009; Finlay et al. 2020), but rarely in the  
810 framework of plant Si nutrition and subsequent positive influence on plant performance or crop  
811 yield. We have stressed the importance of biotic factors such as mycorrhizal associations, SSB,  
812 soil macrofauna, large herbivores and root exudates on soil-plant Si mobility, and suggest  
813 different mechanisms by which these processes may affect Si dynamics and stimulate soil-plant  
814 Si cycling in agroecosystems. The time has come to seriously consider biotic factors, both in  
815 natural and agricultural systems, because Si is involved in numerous functions that contribute to

816 plant performance and stress regulation, which may impact plant productivity and crop yield. We  
817 suggest the following aspects to be considered in the near future:

- 818 1. What is the abundance and diversity of SSB in soils? In which soil types/mineralogy are  
819 they found most? To what extent do SSB contribute to the plant-available Si pool and  
820 subsequent plant Si uptake compared with abiotic mineral weathering, and by what  
821 mechanisms? How do agricultural practices and cropping systems impact SSB abundance,  
822 diversity, and functions?
- 823 2. By which mechanisms do mycorrhizal fungi increase plant Si concentrations? Can plant  
824 Si nutrition be improved through common mycorrhizal networks? Does an increase in  
825 plant Si concentrations as affected by mycorrhizal fungi mostly occur in nutrient-depleted  
826 soils?
- 827 3. To what extent do non-mycorrhizal nutrient-acquisition strategies influence soil Si  
828 mobilization and plant Si uptake? By which mechanisms? If root exudates mobilize Si  
829 from soil minerals, does this occur only in P-depleted soils and without P fertilization?  
830 Can we exploit these strategies to improve crop Si nutrition in cropping systems such as  
831 cereal-legume intercropping?
- 832 4. Is the earthworms-related increase in soil-plant Si mobility significant at soil profile  
833 scales? Do cover crops, intercropping or integrated crop-livestock systems influence this  
834 process by modifying earthworm abundance and diversity?
- 835 5. What is the impact of large herbivores on global Si biogeochemistry? To what extent do  
836 they stimulate soil-plant Si mobility in natural ecosystems and integrated crop-livestock

837 systems? Do integrated crop-livestock systems influence Si dynamics through changes in  
838 microbial community and biomass, soil aggregation or organic matter dynamics?

839 6. Does the long-term recycling of crop residues significantly increase plant-available and  
840 plant Si concentrations, and slow down long-term soil desilication? What are the long-  
841 term advantages and disadvantages of different residue management practices (i.e. direct  
842 incorporation, burning, or biochar/manure/compost production and subsequent  
843 application)? How does decomposition dynamics influence Si release from phytolith  
844 dissolution in different geopedoclimatic contexts, and for different plant species?

845 7. What are the short- and long-term effects of cover crops on soil-plant Si mobility? Can  
846 legume cover crops significantly stimulate Si mobility compared with grass cover crops?  
847 Does the absence of cover crops significantly increase soil phytolith losses through soil  
848 erosion?

849 8. How do soil aggregation and soil structure impact soil-plant Si dynamics? Do *microbial*  
850 *hotspots* in soil aggregate fractions and at surfaces of minerals affect soil Si dynamics and  
851 release into the soil solution? Is it significant at the soil profile scale? How do  
852 modifications of soil structure and aggregation by anthropogenic land transformations  
853 (ploughing, soil pH-induced modification by liming, clay dispersion associated with high  
854 sodium content in saline-sodic soils) influence these processes?

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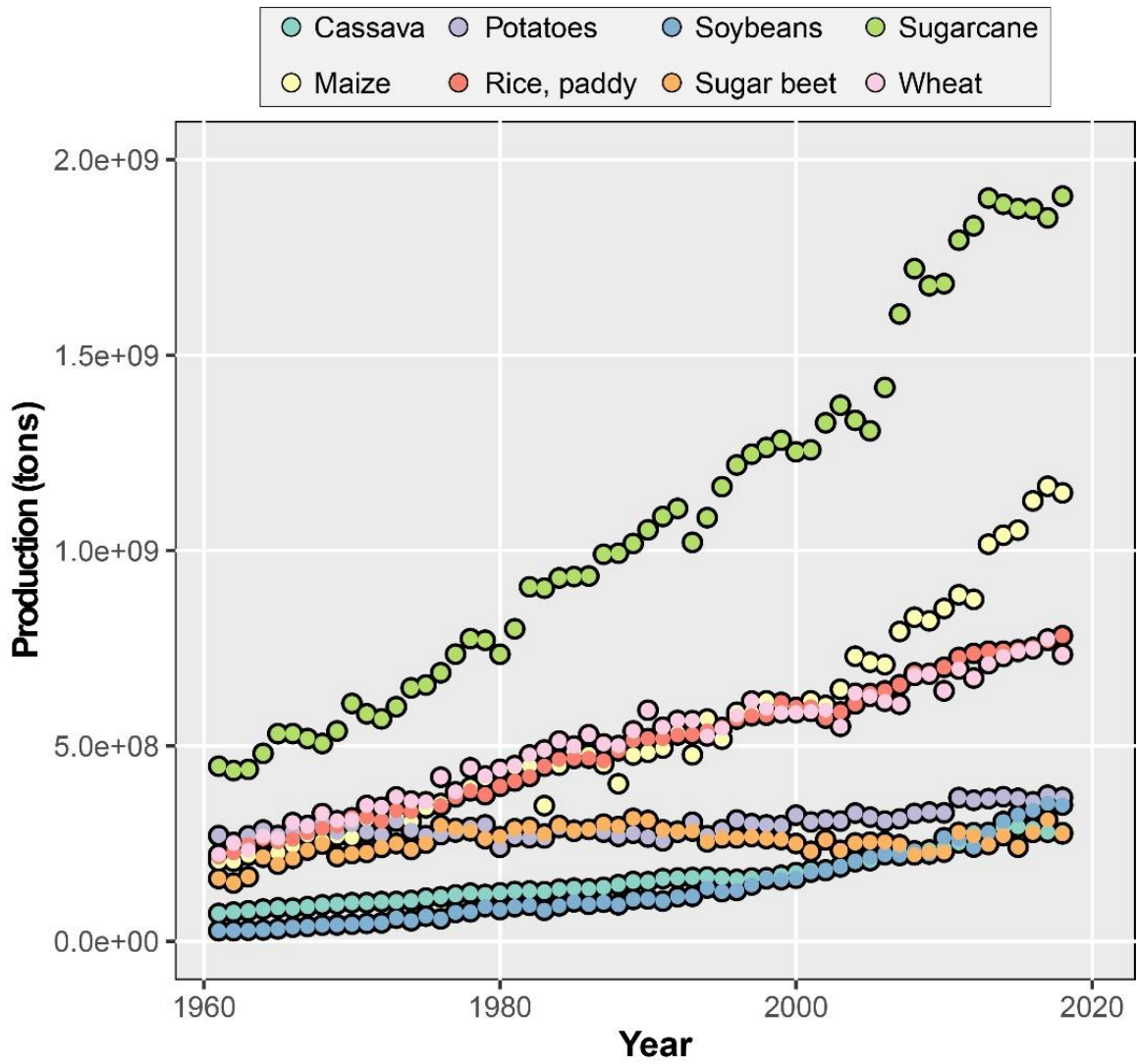
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1756 **Figures**



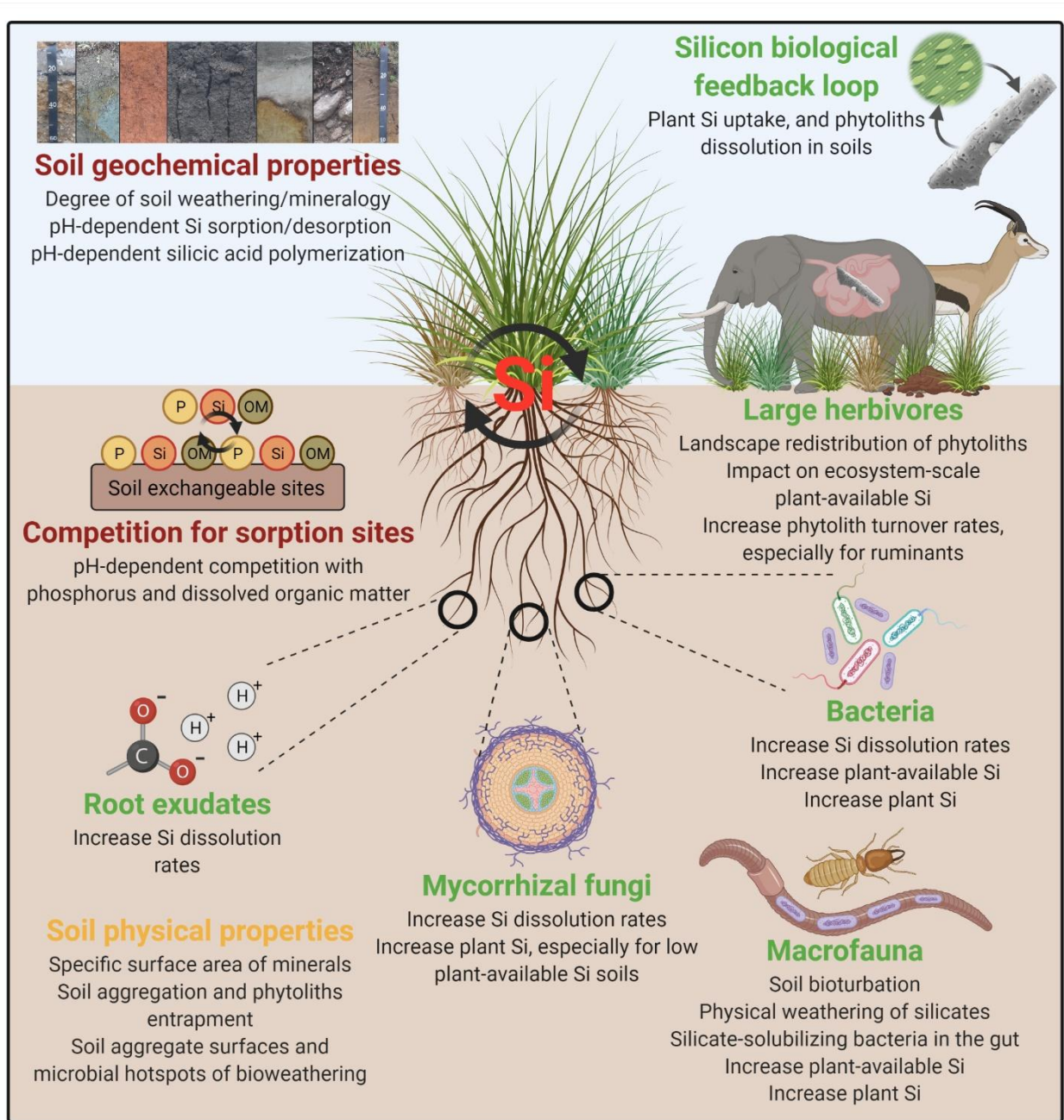


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1758 **Fig. 1** – Global production of the eight most important crops in 2018, from 1961 to 2018 (source  
 1759 = FAOSTAT).

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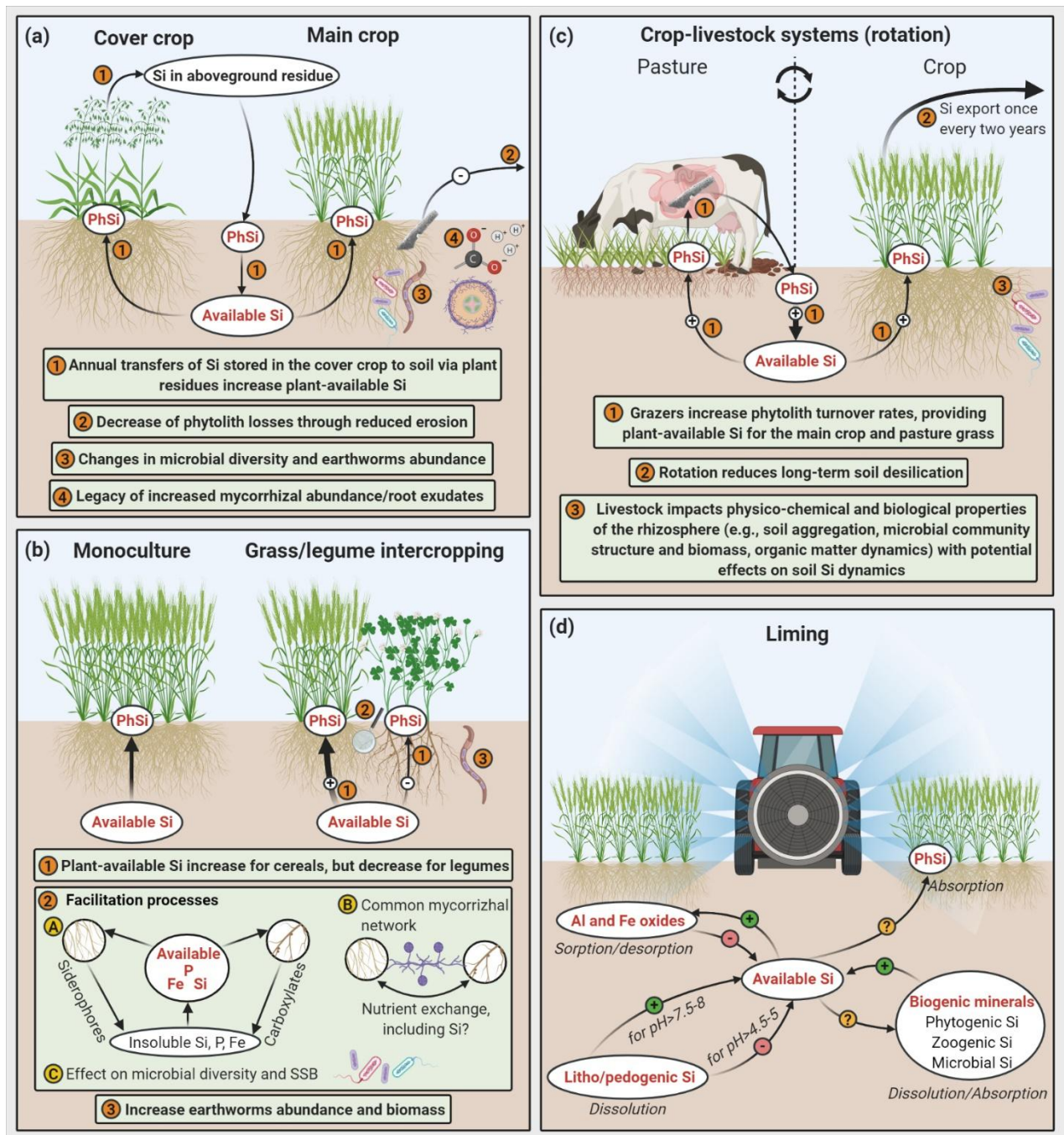
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1763 **Fig. 2** – Biotic and abiotic factors influencing soil-plant Si dynamics. This figure was created

1764 using BioRender.



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1766 **Fig. 3** – Effects of agricultural practices on soil-plant silicon (Si) dynamics. **(a)** The transfer of Si  
 1767 stored in the cover crop to soil via plant residues may substantially increase the soil phytogenic Si  
 1768 pool (PhSi), thus contributing to increase plant-available Si concentrations (available Si) (# 1).

1769 Cover crops could also lower phytolith losses though reduced erosion (Adetunji et al. 2020) (# 2),  
1770 modify microbial diversity and earthworm abundance (Roarty et al. 2017; Euteneuer et al. 2020)  
1771 (# 3), and provide a legacy of increased mycorrhizal abundance/root exudates (Hallama et al.  
1772 2019) (# 4), thereby impacting soil-plant Si dynamics. **(b)** Cereal-legume intercropping may  
1773 increase plant-available Si concentrations for the cereal crops, but decrease it for the legume  
1774 crops (Ning et al. 2017) (# 1). Numerous facilitation processes with beneficial effects on soil-  
1775 plant Si mobility may also occur (# 2): taking advantage of different nutrient-acquisition  
1776 strategies (Li et al. 2014; Xue et al. 2016), sharing nutrients via common mycorrhizal network  
1777 (Walder et al. 2012), or modifying microbial diversity (Brooker et al. 2015), including silicate-  
1778 solubilizing bacteria (SSB). Cereal-legume intercropping may also increase plant-available Si  
1779 concentrations and plant Si uptake through enhanced earthworm abundance and biomass  
1780 (Schmidt et al. 2001, 2003) (# 3). **(c)** Integrating crops and livestock will increase Si release from  
1781 phytoliths in animal dung (Vandevenne et al. 2013), which will provide Si for the main crop and  
1782 pasture grass (# 1). Pasture/crop rotation could also reduce long-term soil desilication by  
1783 reducing Si export from harvest (once every two year) (# 2). Crop-livestock systems modify  
1784 physical, chemical and biological properties of the rhizosphere (Brewer and Gaudin 2020), that  
1785 could, in turn, influence soil-plant Si dynamics (# 3). **(d)** Increase in soil pH after liming  
1786 increases Si adsorption on soil colloids, which, in turn, reduces Si concentrations in the soil  
1787 solution. Raising pH above 4.5-5.0 decreases aluminosilicate dissolution rates, while raising pH  
1788 above 7.5-8.0 increases those rates (Drever 1994; Kelly et al. 1998; Haynes 2019). Raising pH in  
1789 the range 3.0-9.0 increases phytolith dissolution rates (Frayse et al. 2009). The pH/liming effects

1790 on Si absorption by soil living organisms and plants is unknown. This figure was created using  
1791 BioRender.