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Silicon in aquatic vegetation

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21 Summary

- 22 • Silicon (Si) use by plants has not always received the research attention of other elements. Yet
23 today, the importance of Si for plant functioning is slowly becoming better understood. Si is a
24 crucial element for many terrestrial plant species (especially grasses), yet a recent surge of
25 research has shown that some species of aquatic plants contain significant amounts of Si too.
- 26 • We argue that degree of Si accumulation is a functional trait in aquatic vegetation, with plants
27 adapting to environmental conditions. Aquatic vegetation can show apparent plasticity regarding
28 Si-uptake, adaptive to water and wind dynamics, light interception, herbivory and nutrient
29 stress. Beyond a plant physiological viewpoint, high Si uptake results in high BSi in plant litter,
30 which can impact on aquatic decomposition processes. Si content in aquatic vegetation shows
31 intriguing relations with other strength components such as cellulose and lignin. Si content has
32 also been linked to fungal and microbial community, litter stoichiometry and invertebrate
33 shredders: all factors that potentially influence organic turnover in aquatic sediments.
- 34 • Uptake of Si by aquatic vegetation is thus not only an important transient sink for Si in the global
35 biogeochemical Si cycle, it can also affect carbon turnover in aquatic ecosystems. Experimental
36 and field studies should be conducted to elucidate controls on aquatic plant Si uptake, especially
37 focusing on interactive effects of multiple biotic and abiotic factors. This review provides an
38 overview of the state-of-the-art knowledge on silicon in aquatic vegetation.

39 **Main text**

40 A recent surge of research has emphasized that several aquatic species contain significant amounts of
41 biogenic Si (BSi), an amorphous hydrated matrix of Si, in their biomass. Studies have hinted to a
42 functional role of BSi in aquatic vegetation as a strength component (Schoelynck et al. 2010), and the
43 potential biogeochemical impacts of plant Si uptake on litter decomposition (Schaller & Struyf 2013).
44 Wetland plant phytoliths (plant Si bodies) have been linked to substantial storage of occluded C (Li et al.
45 2013a, Li et al. 2013b).

46 In this essay, we argue that plant Si uptake is a functional trait in aquatic vegetation, with plants adapting
47 their Si uptake to environmental conditions, and Si biogeochemistry in turn impacted by plant Si cycling.
48 Our arguments thus consist of three overarching themes: (i) the large variability in BSi concentrations, (ii)
49 the role of Si as a functional trait in aquatic vegetation and (iii) the effect of plant Si uptake on cycling of
50 Si in aquatic systems (biogeochemical implications). Our manuscript supports to the growing conscience
51 that biological Si cycling, in both terrestrial and aquatic ecosystems, exerts a strong control on
52 biogeochemical Si fluxes, and potentially even coupled with carbon cycling (Song et al. 2012).

53 **Large variability in BSi concentrations**

54 There are four main aquatic plant life forms (Janauer, Schmidt-Mumm & Reckendorfer 2013): (i) *free*
55 *floating* on the water surface, (ii) rooting in the sediment, but concentrating the leaves near the water
56 surface (*floating leaved*), (iii) rooted, but obligate submerged (*rooted submerged*), and (iv) *emergent*
57 with only basal stem parts in the water. The first life form (free floating) is the group with the fewest
58 species. We will show that they take up only small amounts of Si. The second life form (floating leaved)
59 concentrates the bulk of its biomass near the water surface optimising irradiance and photosynthesis.
60 Underneath this upper layer of biomass, generally less biomass is present due to self-shading of the
61 leaves (Arts et al. 1988). Their habitats range from stagnant water (ponds and lakes) to relatively slow

62 running water (streams and rivers). Generally, stems are flexible (i.e. not rigid) and surficial leaves are
63 thicker than submerged leaves due to presence of a cuticle with stomata for gas exchange with the air
64 (Maberly & Spence 1989). They rely mainly on their root system for nutrient uptake, though they can
65 sometimes take up dissolved nutrients (including Si) from the water through their shoots (Wigand et al.
66 2001; Madsen & Cedergreen 2002). The third life form (rooted submerged) has in general many, often
67 streamlined leaves and a stem that is flexible. Their habitats range from stagnant water (ponds and
68 lakes) to running water (streams and rivers): some species can occur at stream velocities up to 1 m s^{-1}
69 (Franklin, Dunbar & Whitehead 2008). Being completely submerged, the species are able to take up
70 nutrients (including Si) through both roots and shoots (Madsen et al. 2002). The leaves of the fourth life
71 form (emergent) grow in the air. Plants are generally sturdier than those of other aquatic plant life forms
72 and the stem is generally thicker and more rigid. Emergent species occur in ponds, on lake shores and in
73 shallow wetlands with low standing or very slow flowing water ($<0.1 \text{ m s}^{-1}$; Bal et al. 2011).

74 Due to the different abiotic conditions and different nutrient uptake routes of the four life forms, plants
75 may use available Si differently and the availability of dissolved Si (DSi) in the aquatic environment can
76 play an important role. Schoelynck et al. (2012b) grew *Egeria densa* under variable DSi concentrations,
77 and BSi content in stems and leaves varied accordingly. The Si concentration in the tissues of *E. densa* in
78 response to DSi availability followed a logarithmic curve, with increasing BSi in biomass related to
79 increasing ambient DSi concentrations, until apparent saturation is reached, beyond which biomass BSi
80 concentration stabilized. Schaller et al. (2012b) observed strong increases in tissue concentration of BSi
81 in *Phragmites australis* when supplying amorphous silicon as a Si fertilizer.

82 To quantify the variability in Si accumulation, relative to silicon availability, we have gathered a large
83 dataset of BSi concentrations in aquatic vegetation and of DSi concentrations in the associated aquatic
84 environment (i.e. surface water samples). Our dataset covers all four life forms: 5 free floating species

85 (e.g. *Eichhornia crassipes*), 17 floating leaved species (e.g. *Nymphaea nouchali*), 31 rooted submerged
86 species (e.g. *Myriophyllum aquaticum*) and 30 emergent species (e.g. *Phragmites australis*). In total, we
87 have gathered 233 plant samples from 48 different locations (e.g. ponds, rivers, lakes) in 19 different
88 countries worldwide. Of all samples, 63% of all samples came from Europe, 27% from Africa, 7% from
89 Asia, 3% from South and Central America and <1% from North America (Fig. 1; see Appendix S1 in
90 Supporting Information for detailed results and background information).

91 Differences between growth forms are apparent for both the BSi/DSi ratios (ratio of BSi concentration to
92 surface water DSi concentration of the habitat) and the actual BSi concentrations in the plant. Emergent
93 vegetation and rooted submerged vegetation generally contain higher BSi concentrations than free
94 floating vegetation or floating leaved vegetation. In multiple studies, shoot length and plant age have
95 been highlighted as strong controls on plant BSi content, with BSi content increasing with increasing
96 shoot length (e.g. Norris & Hackney 1999; Struyf et al. 2005; Querné, Regueneau & Poupart 2012). Since
97 there is a large variety of shoot length, this could partly explain the large variability between species, but
98 not between different life forms. Three hypotheses can explain the significantly larger uptake for the
99 emergent and rooted submerged vegetation: (i) presence of Si accumulator species, (ii) higher DSi
100 uptake capacity, and (iii) a larger impact of abiotic stress. The emergent life form has indeed multiple
101 species of the grass family, which are notorious Si accumulators. However, while the other 3 groups
102 don't include grass species, the BSi concentration in the group of rooted submerged species didn't differ
103 from the concentration in the emergent species, making the first hypothesis inconclusive. Regarding the
104 second hypothesis, the large accumulated leaf surface of the many submerged leaves may indeed govern
105 an efficient Si uptake from the aquatic environment, as compared to the three other life forms which
106 rely mainly on their roots for nutrient uptake. However, these two hypotheses do not rule out an effect
107 of stress factors that may trigger Si uptake in the plants. Environmental variables that have been linked

108 to plant Si uptake are hydrodynamic stress, herbivory, and nutrient limitation. In the next section, we
109 give arguments why Si uptake can be considered as a functional trait.

110 **The role of Si as a functional trait in aquatic vegetation**

111 Morphological differences between these four plant life forms are, to a great extent, adaptations to the
112 different environmental conditions and mechanical forces that are dominant in the two media (Hamann
113 & Puijalon 2013; Fig. 2). Free floating species (life form 1) adapt their buoyancy: they are not directly
114 affected by hydrodynamic forces (except for wind and currents moving them around). Submerged
115 species (both growth forms 2 and 3) are positioned within the water column so that the shoots are
116 supported by water. This is achieved by buoyancy of the leaves and an additional lift force that is
117 generated by the current, which counteracts gravity. The current also creates a drag force on the shoot
118 by bouncing against it (form drag) and by a friction between fluid and plant surface (skin drag). These
119 result in a horizontal force that pulls the shoot, to which the plant resists with a given tensile strength.
120 Because of the less densely vegetated zone underneath the floating leaved biomass of life form 2, less
121 interaction with the flow is expected (the water can flow relatively undisturbed), whereas flow is
122 significantly reduced in dense stands of the rooted submerged life form 3 (Puijalon et al. 2011; Janauer
123 et al. 2013). Emergent species (life form 4), with leaves in the air, need to overcome gravity to keep an
124 upright position. Drag forces generated by winds are usually a few orders of magnitude lower than those
125 generated by water (because of lower viscosity), yet high wind speeds, or waves, can cause drag forces
126 that bend the shoot down (vertically). The plant resists with a given bending strength (Silinski et al.
127 2015).

128 In the light of all the different forces acting upon aquatic plants, it is not surprising that the functional
129 role of BSi as a structural component providing rigidity has received attention. However, other functional
130 roles of Si uptake in aquatic macrophytes have also been reported, including response to light
131 interception, herbivory, and nutrient stress. Studies have particularly targeted the rooted submerged

132 species *Egeria densa*, *Elodea canadensis* and *Limnophila heterophylla*, *Nuphar lutea* which is a floating
133 leaved species with a significant submerged biomass (intermediate between life forms 2 and 3), and
134 emergent genera *Spartina* and *Phragmites*.

135 Hydrodynamic stress

136 Submerged species (floating leaved or rooted submerged) growing in riverine or stream environments,
137 are directly exposed to flow stress. It is therefore not surprising that studies, although limited in number,
138 have shown that some aquatic species adapt to increased flow dynamics by increasing DSi uptake. For
139 example, under experimental conditions the rooted submerged species *Egeria densa* and *Limnophila*
140 *heterophylla* had higher BSi concentrations when exposed to higher flow velocities (Schoelynck et al.
141 2012b; Schoelynck et al. 2014). Plants also showed higher BSi content with higher DSi availability,
142 showing that higher ambient Si-availability facilitates macrophyte Si uptake. Similar results were found
143 for *Nuphar lutea* growing *in situ* (Schoelynck et al, 2014), where its submerged leaves and stems had
144 higher BSi content in streams compared to oxbow lakes (with reduced flow stress). Plant stem
145 resistance, which is the plant's ability to minimize the negative impact of environmental adverse
146 conditions, is based either on avoidance or tolerance (Puijalon et al. 2011). A negative relationship
147 between BSi in aquatic macrophytes and cellulose concentration has been observed across a wide
148 number of species for the Biebrza river valley in Poland (Schoelynck et al. 2010), confirming that Si is a
149 potentially cheap alternative for cellulose (Raven et al. 1983). Interestingly, an apparent positive
150 correlation between cellulose and BSi content in emergent species was observed also (Schoelynck et al.
151 2010), which suggests that the relationship between BSi and lignocellulose depends on plant growth
152 form. Schaller, Brackhage & Dudel (2012) showed that the availability of BSi in *Phragmites australis*
153 affected the cellulose content differently according to the function of the tissue. BSi reduced cellulose
154 content in tissues that play a role in plant stability (culm), but increased cellulose content in tissues

155 where stability function is of lesser importance (leaves). Vretare et al. (2001) showed increased stem
156 weight of *Phragmites australis* at sandy sites with heavier wind and wave action, linking this to
157 potentially higher Si concentrations in the tissue. Increased stem weight was part of a phenotypically
158 plastic response to water depth. In Table 1 we have summarized these studies on BSi, lignin and cellulose
159 in aquatic vegetation, showing that trends observed in different plant species were not always
160 consistent, probably because of different sampling strategies (lumped biomass vs. individual leaves or
161 stems), different experimental setups, or because plants just respond differently. The exact mechanisms
162 behind these correlations have not been uncovered.

163 The arguments we demonstrate here are in accordance with Fig. 1. The emergent species and the rooted
164 submerged species may generally have a tolerance strategy (*sensu* Puijalon et al. 2011) and need to
165 invest in strength to overcome different abiotic forces: emergent species need to overcome a vertical
166 (bending) force (gravity), submerged species a horizontal (pulling) force (the drag force, encountered in
167 unidirectional steady flow (Vogel 2003)). Free floating species, or floating leaved species are less affected
168 by hydrodynamic stress and may generally have an avoidance strategy (*sensu* Puijalon et al. 2011): the
169 leaves float on the water surface and the majority of the water is discharged underneath where little
170 biomass is present (Janauer et al. 2013). This avoidance - tolerance strategies trade-off has important
171 ecological and evolutionary consequences (Puijalon et al. 2011), and it is clear that Si uptake should be
172 considered as an important functional trait with knock-on effects to these strategies.

173 Light interception

174 However, as we stated earlier, hydrodynamic stress is not the only abiotic factor that may affect BSi,
175 cellulose and lignin. Early research indicated the importance of silicification in *Phragmites australis* (Lau
176 et al. 1978). Cuticular deposits on laminae and sheaths protect the shoot against predator attack and (or)
177 water loss, and also provide support during internodal growth. Si in long epidermal cells provides extra

178 support to the shoots, and could also serve as “silica windows”, focusing light onto the photosynthetic
179 mesophyll tissue. The silica windows hypothesis was recently demonstrated for several grass and sedge
180 species including the emergent macrophyte species *Phragmites australis* and *Phalaris arundinacea*
181 (Klančnik, Vogel-Mikuš & Gabersčik 2014). Lau et al. (1978) indicated a similar mechanism in sugar cane
182 (*Saccharum officinarum*, not an aquatic species): more light was transmitted through the silica cells than
183 through other types of epidermal cells. In contrast, Agarie et al. (1996) indicated no effect of leaf
184 silicification on optical properties of leaf transmittance, reflectance and absorbance spectra in rice.
185 Klančnik et al. (2014) concluded that near-surface silicified leaf structures in grasses and sedges (e.g.,
186 prickly hairs, cuticle, epidermis) were essential in affecting the photosynthetic properties, with more
187 detailed localisation studies of Si in plant tissue needed to define the incidence of Si distribution within
188 the different leaf layers and in the different structures, and how this affects their capacity as “silica
189 windows”.

190 Herbivory

191 One study has shown that grass carp herbivory of rooted submerged *Elodea canadensis* was negatively
192 correlated to increasing Si content, but did not investigate whether the plant species specifically adapted
193 to herbivory by higher Si uptake (Bonar et al. 1990). Interestingly, higher cellulose content was also
194 correlated with lower herbivory: in this study, cellulose content of *Elodea canadensis* was the highest in
195 plants with highest Si concentration (Bonar et al. 1990). We have an unpublished dataset showing a
196 negative correlation between BSi content and herbivory by the water lily beetle (*Galerucella nymphaeae*)
197 and dung fly (*Hydromyza livens*) for *Nuphar lutea*, a submerged species with floating leaves (Fig. 3).
198 Floating leaves (n= 23) were collected in the summer of 2010 in the Biebrza river, Poland. Though our
199 dataset is still rather limited and needs further investigation, the same negative correlation between BSi
200 deficiency and gall-making flies and midges was discussed earlier for emergent plants. Tschardtke (1999)
201 showed that reed plants growing in nutrient deprived areas had less BSi, and were at the same time

202 more susceptible to gall formation by a gall-making midge, *Giraudiella inclusa*. In this study, the BSi
203 content was not a response to the presence of the midge, but rather a result of lower Si availability in
204 the growing environment. De Bruyn (1994) suggested a similar mechanism for the gall-forming fly *Lipara*
205 *lucens*, indicating that gall-forming species apparently select thin stressed shoots to avoid host-plant
206 resistance.

207 Nutrient stress

208 Actual phenotypic plasticity of plant Si uptake was suggested for the genus *Spartina* (Carey & Fulweiler
209 2014). These authors hypothesized, based on available field data, that the mode of Si uptake by *Spartina*
210 is dependent on local environmental factors and genetic origin, supporting the idea that the plant
211 species shows a potential spectrum of adaptable Si uptake mechanisms. Active accumulation was
212 suggested for native species exhibiting strong environmental stress conditions. High N content and P-
213 limitation in the stressed environment potentially caused the active accumulation. This corroborates to
214 the suggestion by Meyerson, Vogt & Chambers (2000) that active plant Si uptake results in the strong
215 accumulation of Si in plant litter layers, reducing P-availability to competing species. In another marsh
216 study in two New England marshes (USA) (Carey & Fulweiler 2013), it was shown that also drought and
217 temperature stress caused increased Si accumulation in the tidal marsh grasses.

218 In essence, all these studies point to plasticity regarding Si accumulation, where Si uptake is increased in
219 response to wave and wind dynamics, light interception, herbivory, and nutrient stress. Still, mechanisms
220 are not well understood, and other factors will further determine BSi uptake into emergent species. In a
221 field study in the Bay of Brest (Querné et al. 2012), BSi content in *Spartina* did not show an increase with
222 increasing abiotic stresses, but was strongly correlated with growth and plant length.

223 **Biogeochemical implications**

224 Aquatic vegetation plays an important role in the biogeomorphology and biogeochemistry of aquatic
225 ecosystems. Positive feedback mechanisms within plant patches cause favorable growth conditions, such
226 as increased sedimentation, increased input of nutrients and reduced flow velocity, with reduced risk for
227 breakage or dislodgement. Outside the patches, negative feedbacks (i.e. higher flow velocity and
228 reduced nutrient availability) often prevent the growth of aquatic vegetation. These scale-dependent
229 feedbacks result in self-organized mosaics of vegetated and non-vegetated areas, and associated a
230 mosaic of low-organic and high-organic soil (Schoelynck et al. 2012).

231 Carey & Fulweiler (2012) estimated annual uptake of BSi into wetland vegetation at $4.16 \text{ Tmole a}^{-1}$. This
232 was based on an average BSi concentration of 0.62 % Si. This average is similar to our average in riverine
233 vegetation ($0.49 \pm 0.04 \%$). The uptake constitutes about 60% of annual riverine transport of Si into the
234 coastal zone and the ocean (Tréguer & De la Rocha 2013). It is unclear whether the estimate in Carey et
235 al. (2012) includes only emergent species, or also other growth types, but the rough estimate does show
236 that aquatic vegetation forms an important transient sink for Si passing through rivers. Two studies have
237 pointed to a significant presence of phytoliths in swamp soils (Cary et al. 2005; Li et al. 2013a), with the
238 carbon occluded in the phytoliths of wetland plant species potentially an important sink to consider in
239 the carbon cycle (Li et al. 2014). It is crucial to understand the recycling rate of Si from plant litter in
240 aquatic ecosystems, and the potential effect of Si on the decomposition rates. Exemplary to this is the
241 strong (permanent) Si sink in the Okavango Delta sediments (Botswana) that can be associated with a
242 dominance of tropical giant-grasses such as *Cyperus papyrus* (Struyf et al. 2015).

243 The recycling rate of aquatic vegetation associated BSi is currently understudied. To our knowledge, only
244 experiments on *Phragmites australis* litter have been performed, and initial field observations in tidal
245 marshes showed rapid recycling of reed phytoliths, with all Si dissolved from the litter within one year
246 (Struyf et al. 2007). Data on other species and in other less dynamic environments (tidal marshes receive

247 fresh flood water multiple times during a spring-neap tide cycle) are needed to constrain whether rapid
248 recycling of aquatic vegetation related Si is a rule or an exception.

249 The spatial pattern of aquatic vegetation also exerts an important effect on patterns of sedimentation
250 and erosion in rivers (Schoelynck et al. 2012). By slowing down the current, macrophyte patches enhance
251 sedimentation inside and downstream of their canopy. Studies report accumulation of organic matter in
252 macrophyte patches up to 12 times (Sand-Jensen 1998; Cotton et al. 2006), 2.9 to 4.2 times (Kleeberg et
253 al. 2010) and up to 6 times (Schoelynck et al. 2015) more compared to non-vegetated sediments. It is
254 likely that BSi is also accumulated in the macrophyte patches.

255 There is now growing evidence that such Si incorporation in plants and thus in the deposited litter, being
256 controlled by availability, or by any mechanism that stimulates increased Si accumulation, is an
257 important control on riparian decomposition rates, and thus on the role of aquatic systems in the
258 sequestration of carbon. Schoelynck et al. (2010) and Schaller et al. (2012) clearly showed a strong
259 interdependence of BSi content and biomass content of lignin and/or cellulose, two components that are
260 important for litter stability and decay rates. Interestingly, Si uptake in aquatic vegetation was also
261 shown to affect C/N/P ratios in the litter biomass (Schaller et al. 2012; Schaller et al. 2015). This means
262 there is a direct effect of Si content in wetland and aquatic vegetation on litter quality and thus
263 decomposition dynamics. In a decomposition experiment with Si rich litter and Si poor litter from
264 *Phragmites australis*, interactive effects of shredder abundance and Si content on decomposition rates
265 were observed. In the absence of shredders, litter high in BSi content showed largest decomposition
266 rates and fastest carbon turnover rates. The authors hypothesized that ambient Si availability could
267 impact positively on growth of fungi and bacteria (Schaller et al. 2013). In addition, resulting from the
268 rapid dissolution of amorphous Si deposits from the litter (Struyf et al. 2007), they hypothesized that the

269 surface area of the leaves may increase due to the removal of silicon double layers in the surface near
270 area.

271 In the same experiment (Schaller et al, 2013), in the presence of macro-invertebrate shredders,
272 decomposition rates actually decreased when litter was more Si rich. This points to a negative effect of Si
273 uptake in vegetation on shredder functionality, and thus on total decomposition rates in aquatic and
274 wetland systems. The authors hypothesized that the invertebrates may be deterred of feeding on leaf
275 litter by the high amount of phytoliths, as described for folivores, for which high density of phytoliths in
276 the food results in enhanced mandible wear (Massey & Hartley 2009). It is clear that an effect of
277 vegetation BSi on decomposition rates of riparian litter is apparent in at least one aquatic vegetation
278 species (*Phragmites australis*), but lack of research on other plant species and vegetation, and also a
279 strong lack of field evidence, prevents any current accurate quantification of this effect. In a more recent
280 study, Schaller et al. (2014) showed that detrimental effects of Si on fungal decomposers, were
281 potentially compensated for by other members of the microbial community that profited from high Si
282 availability.

283 **Synthesis**

284 Given the potential importance of Si uptake as a functional trait, and the important biogeochemical
285 consequences Si uptake can have for aquatic and wetland ecosystems, experimental and field studies are
286 needed to further elucidate controls on aquatic plant Si uptake, especially focusing on interactive effects
287 of multiple factors. Such factors can include the abiotic and biotic characteristics suggested above, in
288 experimental setups, as current evidence is mostly observational. It should be noted that current
289 research is limited to a small number of species, and a broader phylogenetic coverage would be
290 beneficial. We hope this essay can stimulate the expansion of the research community studying Si cycling

291 in aquatic vegetation: despite its strong importance for both the plants and the biogeochemical cycle,
292 the number of researchers studying this topic has remained limited.

293

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300 Data Accessibility

301 All data used in this manuscript are present in the manuscript and its supporting information.

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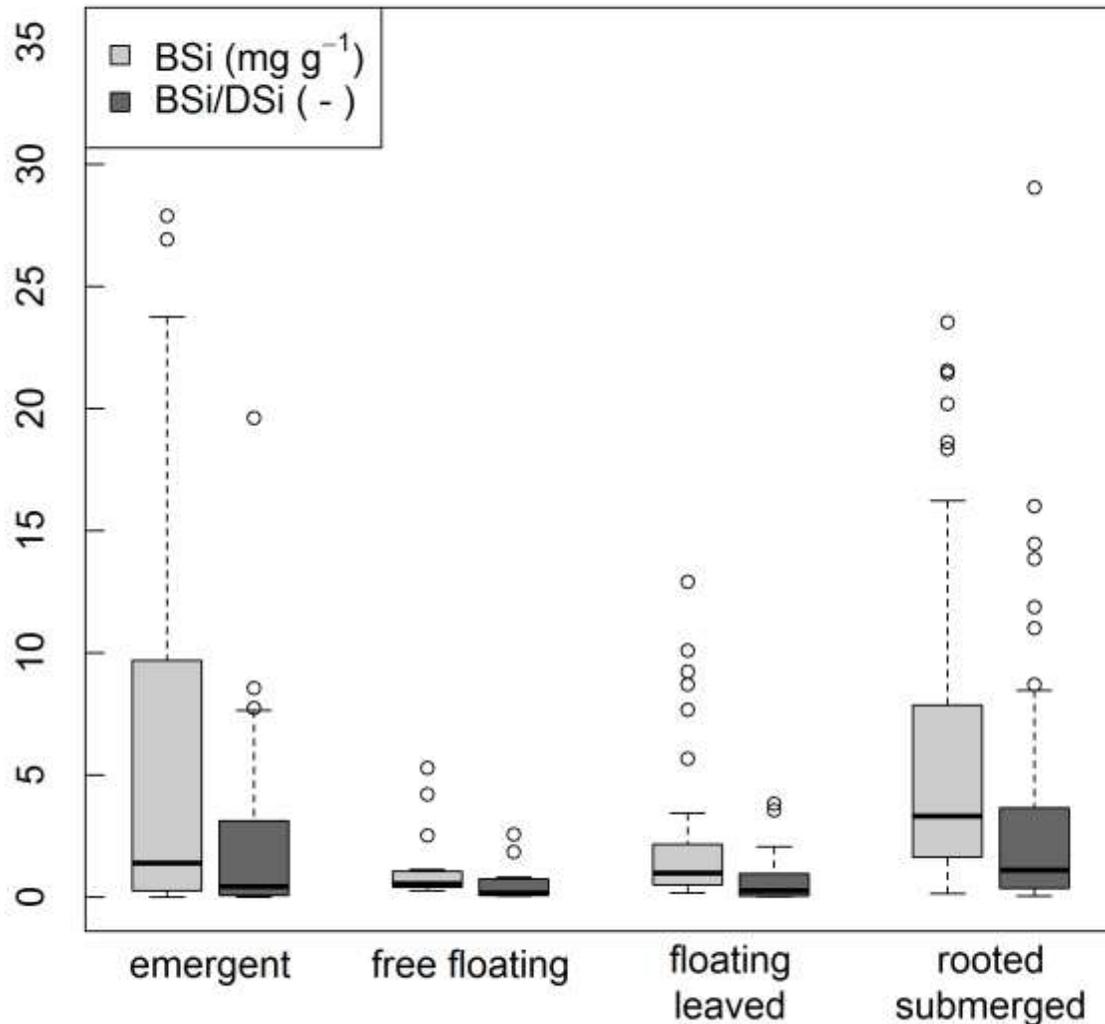
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424 **Supporting information**

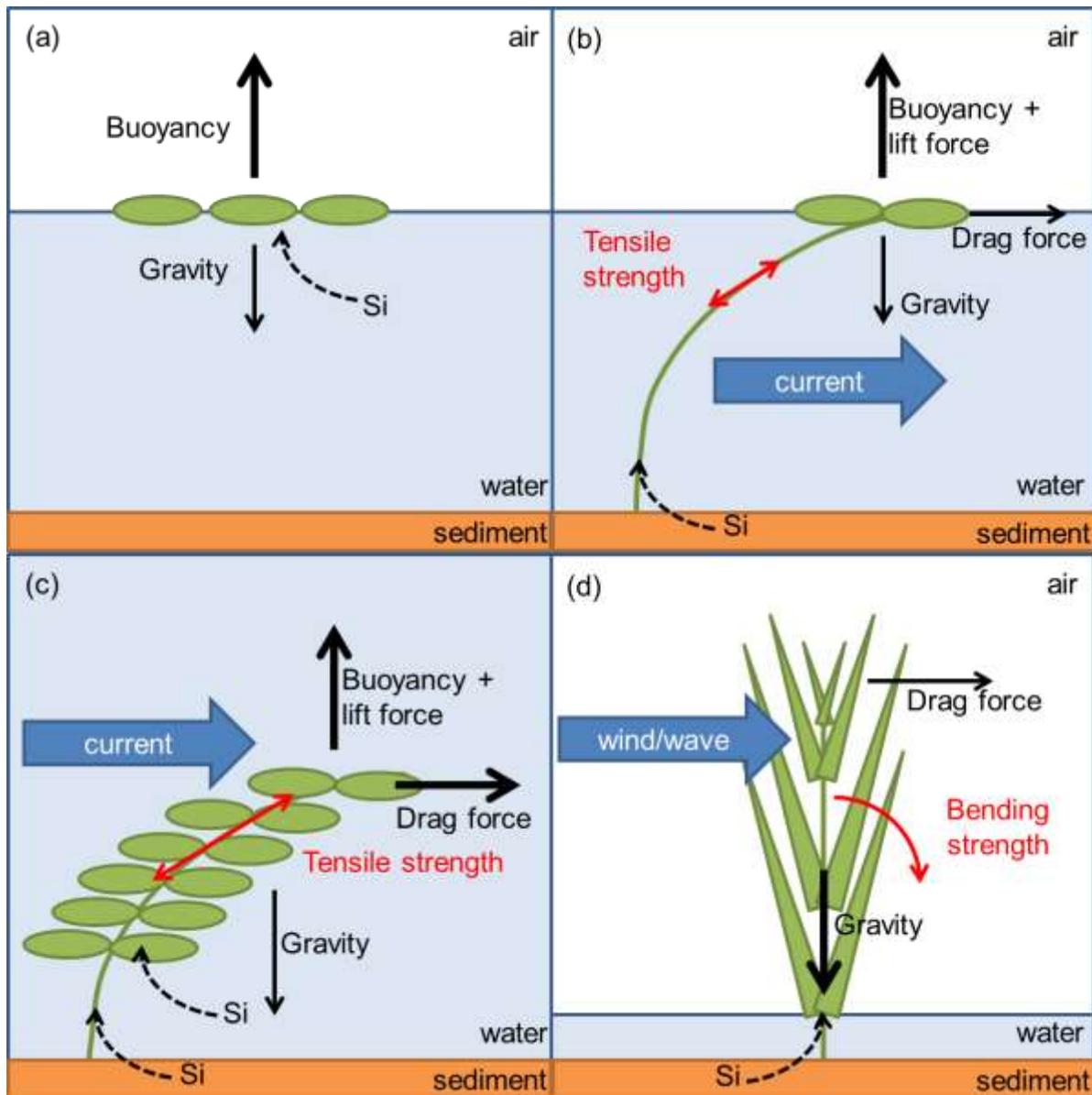
425 Additional supporting information may be found in the online version of this article.

426 Appendix S1 Detailed dataset and background information of Figure 1

427 **Figures and captions**

428

429 **Figure 1:** Boxplot of the median BSi concentrations (mg BSi g⁻¹ DM) and the average ratio of plant BSi
 430 over the ambient DSi concentration (-) for each macrophyte life form (+ 95 percentile confidential
 431 interval). Average BSi concentration is significantly different between emergent and floating leaved
 432 species, between rooted submerged and floating leaved species and between rooted submerged and
 433 free floating species. Average BSi/DSi ratio is significantly different between rooted submerged and
 434 floating leaved species. (R version 3.2; p<0.05, one-way ANOVA followed by a post-hoc Tukey HSD
 435 correction).



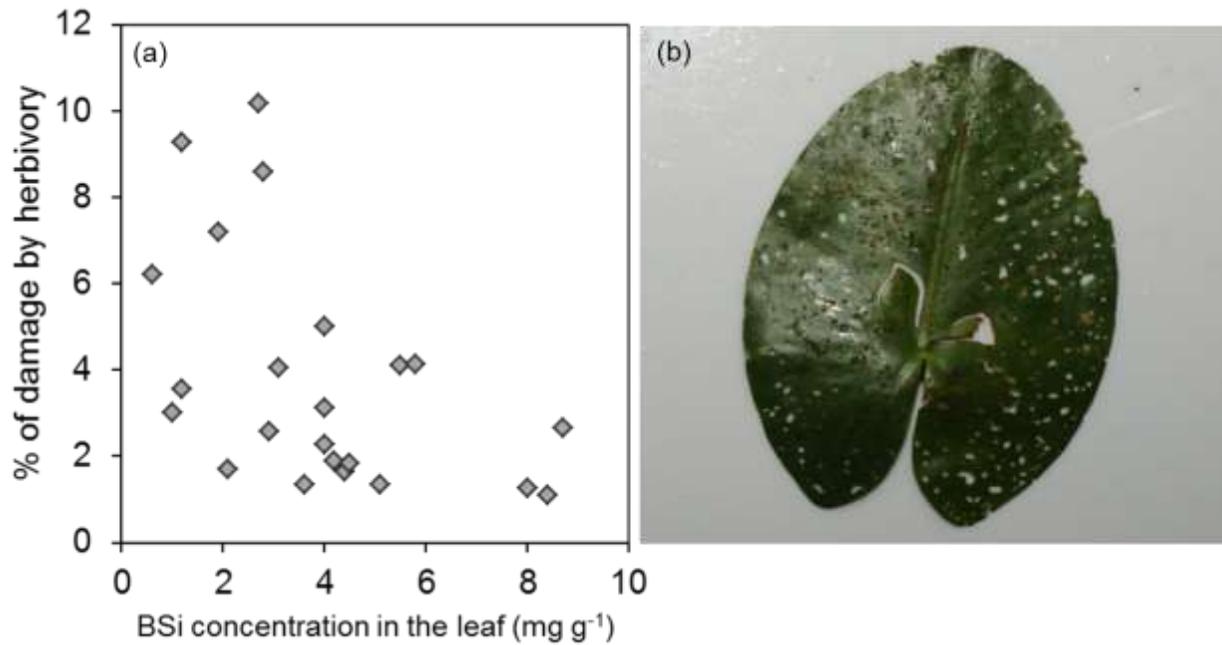
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437 **Figure 2:** Schematic overview of the main mechanical forces (black arrows) that act upon (a) free floating
 438 macrophytes, (b) floating leaved macrophytes, (c) rooted submerged macrophytes, and (d) emergent
 439 macrophytes). Red arrows indicate the main strength properties (tensile strength is horizontal, bending
 440 strength is vertical) and dashed lines indicate the main uptake routes for silica. The size of the arrows is
 441 indicative for the main direction of the forces within each panel representing a different life form, but
 442 cannot be compared between panels because this depends on the actual size of the species.

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447 **Figure 3:** (a) Negative linear relation between floating leaf silica concentration (in mg g⁻¹) of *Nuphar lutea*
 448 (L.) Sm. and the herbivory damage (in % of the total leaf surface). $R^2=0.24$, $p=0.016$, Pearson's correlation
 449 test. (b) Top view picture of a floating leaf with many small circular holes caused by *Galerucella*
 450 *nymphaeae*, and 2 U-shaped holes likely caused by *Hydromyza livens*.

451 **Table 1: Overview of the significant relations between plant silica and cellulose and between silica and**
 452 **lignin for all studied macrophyte species.** RS = rooted submerged, FL = floating leaved, E = emergent, + =
 453 significant positive relation between components, - = significant negative relation between components,
 454 0 = no significant effect reported in the study.

Species	Life form	Si - Cellulose	Si - Lignin	Comment	Study
Submerged species in general	RS, FL	-	0	Field conditions	Schoelynck et al. (2010)
<i>Nuphar lutea</i>	RS	-	+	Field conditions	Schoelynck et al. (2012)
<i>Egeria densa</i>	RS	0	+	Experiment with hydrodynamic stress	Schoelynck et al. (2015)
Emergent species in general	E	+	-	Field conditions	Schoelynck et al. (2010)
<i>Oryza sativa</i>	E	-	-	Experiment; only in leaf blade	Bonilla (2001)
<i>Scirpus maritimus</i>	E	-	+	Experiment	Heuner et al. (2015)
<i>Scirpus maritimus</i>	E	0	+	Field conditions	Silinski (2015)
<i>Scirpus tabernaemontani</i>	E	-	+	Experiment	Heuner et al. (2015)
<i>Phragmites australis</i>	E	-	0	When tissue has a stabilization function	Schaller et al. (2012)
<i>Phragmites australis</i>	E	+	0	When tissue has no stabilization function	Schaller et al. (2012)

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