Summary

1. Silicon (Si) use by plants has not always received the research attention of other elements. Yet today, the importance of Si for plant functioning is slowly becoming better understood. Si is a crucial element for many terrestrial plant species (especially grasses), yet a recent surge of research has shown that some species of aquatic plants contain significant amounts of Si too.

2. We argue that degree of Si accumulation is a functional trait in aquatic vegetation, with plants adapting to environmental conditions. Aquatic vegetation can show apparent plasticity regarding Si uptake, adaptive to water and wind dynamics, light interception, herbivory and nutrient stress. Beyond a plant physiological viewpoint, high Si uptake results in high BSi in plant litter, which can impact on aquatic decomposition processes. Si content in aquatic vegetation shows intriguing relations with other strength components such as cellulose and lignin. Si content has also been linked to fungal and microbial community, litter stoichiometry and invertebrate shredders: all factors that potentially influence organic turnover in aquatic sediments.

3. Uptake of Si by aquatic vegetation is thus not only an important transient sink for Si in the global biogeochemical Si cycle, it can also affect carbon turnover in aquatic ecosystems. Experimental and field studies should be conducted to elucidate controls on aquatic plant Si uptake, especially focusing on interactive effects of multiple biotic and abiotic factors. This review provides an overview of the state-of-the-art knowledge on silicon in aquatic vegetation.

Key-words: abiotic stress, biogenic silicon, cellulose, decomposition, lignin, macrophytes, plant strength

Introduction

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

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

Large variability in BSi concentrations

There are four main aquatic plant life forms (Janauer, Schmidt-Mumm & Reckendorfer 2013): (i) free floating on the water surface, (ii) rooting in the sediment, but concentrating the leaves near the water surface (floating leaved), (iii) rooted, but obligate submerged (rooted submerged), and (iv) emergent with only basal stem parts in the water. The first life form (free floating) is the group with the fewest species. We will show that they take up only small amounts of Si. The second life form (floating leaved) concentrates the bulk of its biomass near the water surface optimizing irradiance and photosynthesis. Underneath this upper layer of
biomass, generally less biomass is present due to self-shading of the leaves (Arts et al. 1988). Their habitats range from stagnant water (ponds and lakes) to relatively slow running water (streams and rivers). Generally, stems are flexible (i.e. not rigid) and surficial leaves are thicker than submerged leaves due to presence of a cuticle with stomata for gas exchange with the air (Maberly & Spence 1989). They rely mainly on their root system for nutrient uptake, though they can sometimes take up dissolved nutrients (including Si) from the water through their shoots (Wigand et al. 2001; Madsen & Cedergreen 2002). The third life form (rooted submerged) has in general many, often streamlined leaves and a stem that is flexible. Their habitats range from stagnant water (ponds and lakes) to running water (streams and rivers): some species can occur at stream velocities up to 1 m s−1 (Franklin, Dunbar & Whitehead 2008). Being completely submerged, the species are able to take up nutrients (including Si) through both roots and shoots (Madsen & Cedergreen, 2002). The leaves of the fourth life form (emergent) grow in the air. Plants are generally sturdier than those of other aquatic plant life forms, and the stem is generally thicker and more rigid. Emergent species occur in ponds, on lake shores and in shallow wetlands with low standing or very slow flowing water (<0.1 m s−1; Bal et al. 2011).

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

To quantify the variability in Si accumulation, relative to silicon availability, we have gathered a large data set of BSi concentrations in aquatic vegetation and of DSi concentrations in the associated aquatic environment (i.e. surface water samples). Our data set covers all four life forms: five free floating species (e.g. Eichhornia crassipes), 17 floating leaved species (e.g. Nymphaea nouchali), 31 rooted submerged species (e.g. Myriophyllum aquaticum) and 30 emergent species (e.g. P. australis). In total, we have gathered 233 plant samples from 48 different locations (e.g. ponds, rivers, lakes) in 19 different countries world-wide. Of all samples, 63% of all samples came from Europe, 27% from Africa, 7% from Asia, 3% from South and Central America and <1% from North America (Fig. 1; see Appendix S1, Supporting Information for detailed results and background information). Differences between growth forms are apparent for both the BSi/DSi ratios (ratio of BSi concentration to surface water DSi concentration of the habitat) and the actual BSi concentrations in the plant. Emergent vegetation and rooted submerged vegetation generally contain higher BSi concentrations than free floating vegetation or floating leaved vegetation. In multiple studies, shoot length and plant age have been highlighted as strong controls on plant BSi content, with BSi content increasing with increasing shoot length (e.g. Norris & Hackney 1999; Struyf et al. 2005; Querné, Raguenau & Poupard 2012). Since there is a large variety of shoot length, this could partly explain the large variability between species, but not between different life forms. Three hypotheses can explain the significantly larger uptake for the emergent and rooted submerged vegetation: (i) presence of Si accumulator species, (ii) higher DSi uptake capacity and (iii) a larger impact of abiotic stress. The emergent life form has indeed multiple species of the grass family, which are notorious Si accumulators. However, while the other three groups do not include grass species, the BSi concentration in the group of rooted submerged species did not differ from the concentration in the emergent species, making the first hypothesis inconclusive. Regarding the second hypothesis, the large accumulated leaf surface of the many submerged leaves may indeed govern an efficient Si uptake from the aquatic environment, as compared to the three other life forms which rely mainly on their roots for nutrient uptake. However, these two hypotheses do not rule out an effect of stress factors that may trigger Si uptake in the plants.
Environmental variables that have been linked to plant Si uptake are hydrodynamic stress, herbivory and nutrient limitation. In the next section, we give arguments why Si uptake can be considered as a functional trait.

The role of Si as a functional trait in aquatic vegetation

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

In the light of all the different forces acting upon aquatic plants, it is not surprising that the functional role of BSi as a structural component providing rigidity has received attention. However, other functional roles of Si uptake in aquatic macrophytes have also been reported, including response to light interception, herbivory and nutrient stress. Studies have particularly targeted the rooted submerged species *E. densa*, *Elodea canadensis* and *Limnophila heterophylla*, *Nuphar lutea*, which is a floating leaved species with a significant submerged biomass (intermediate between life forms 2 and 3), and emergent genera *Spartina* and *Phragmites*.

**HYDRODYNAMIC STRESS**

Submerged species (floating leaved or rooted submerged) growing in riverine or stream environments are directly exposed to flow stress. It is therefore not surprising that studies, although limited in number, have shown that some aquatic species adapt to increased flow dynamics by
increasing DSi uptake. For example, under experimental conditions the rooted submerged species *E. densa* and *L. heterophylla* had higher BSi concentrations when exposed to higher flow velocities (Schoelynck et al. 2012b, 2013). Plants also showed higher BSi content with higher DSi availability, showing that higher ambient Si-availability facilitates macrophyte Si uptake. Similar results were found for *N. lutea* growing *in situ* (Schoelynck et al. 2013), where its submerged leaves and stems had higher BSi content in streams compared to oxbow lakes (with reduced flow stress). Plant stem resistance, which is the plant’s ability to minimize the negative impact of environmental adverse conditions, is based either on avoidance or on tolerance (Puijalon et al. 2011). A negative relationship between BSi in aquatic macrophytes and cellulose concentration has been observed across a wide number of species for the Biebrza river valley in Poland (Schoelynck et al. 2010), confirming that Si is a potentially cheap alternative for cellulose (Raven et al. 1983). Interestingly, an apparent positive correlation between cellulose and BSi content in emergent species was observed also (Schoelynck et al. 2010), which suggests that the relationship between BSi and lignocellulose depends on plant growth form. Schaller, Brackhage & Dudel (2012a) showed that the availability of BSi in *P. australis* affected the cellulose content differently according to the function of the tissue. BSi reduced cellulose content in tissues that play a role in plant stability (culm), but increased cellulose content in tissues where stability function is of lesser importance (leaves). Vretare et al. (2001) showed increased stem weight of *P. australis* at sandy sites with heavier wind and wave action, linking this to potentially higher Si concentrations in the tissue. Increased stem weight was part of a phenotypically plastic response to water depth. In Table 1, we have summarized these studies on BSi, lignin and cellulose in aquatic vegetation, showing that trends observed in different plant species were not always consistent, probably because of different sampling strategies (lumped biomass vs. individual leaves or stems), different experimental set-ups or because plants just respond differently. The exact mechanisms behind these correlations have not been uncovered.

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

**LIGHT INTERCEPTION**

However, as we stated earlier, hydrodynamic stress is not the only abiotic factor that may affect BSi, cellulose and lignin. Early research indicated the importance of silicification in *P. australis* (Lau et al. 1978). Cuticular deposits on laminae and sheaths protect the shoot against predator attack and (or) water loss, and also provide support during internodal growth. Si in long epidermal cells provides extra support to the shoots, and could also serve as ‘silica windows’, focusing light onto the photosynthetic mesophyll tissue. The silica windows hypothesis was recently demonstrated for several grass and sedge species including the emergent macrophyte species *P. australis* and *Phalaris arundinacea* (Klánčnik, Vogel-Mikuš & Gaberschik 2014). Lau et al. (1978) indicated a similar mechanism in sugar cane (*Saccharum officinarum*, not an aquatic species): more

### Table 1. Overview of the significant relations between plant silica and cellulose and between silica and lignin for all studied macrophyte species

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

RS, rooted submerged; FL, floating leaved; E, emergent; +: significant positive relation between components; \(-\) significant negative relation between components; 0: no significant effect reported in the study.
light was transmitted through the silica cells than through other types of epidermal cells. In contrast, Agarizel et al. (1996) indicated no effect of leaf silification on optical properties of leaf transmittance, reflectance and absorbance spectra in rice. Klancnik, Vogel-Mikus & Gaberscek (2014) concluded that near-surface silified leaf structures in grasses and sedges (e.g., prickle hairs, cuticle, epidermis) were essential in affecting the photosynthetic properties, with more detailed localization studies of Si in plant tissue needed to define the incidence of Si distribution within the different leaf layers and in the different structures, and how this affects their capacity as ‘silica windows’.

HERBIVORY

One study has shown that grass carp herbivory of rooted submerged E. canadensis was negatively correlated to increasing Si content, but did not investigate whether the plant species specifically adapted to herbivory by higher Si uptake (Bonar et al. 1990). Interestingly, higher cellulose content was also correlated with lower herbivory; in this study, cellulose content of E. canadensis was the highest in plants with highest Si concentration (Bonar et al. 1990). We have an unpublished data set showing a negative correlation between BSi content and herbivory by the water lily beetle (Galerucella nymphaeae) and dung fly (Hydromyza livens) for N. lutea, a submerged species with floating leaves (Fig. 3). Floating leaves (n = 23) were collected in the summer of 2010 in the Biebrza river, Poland. Though our data set is still rather limited and needs further investigation, the same negative correlation between BSi deficiency and gall-making flies and midges was discussed earlier for emergent plants. Tscharntke (1989) showed that reed plants growing in nutrient deprived areas had less BSi, and were at the same time more susceptible to gall plants growing in nutrient deprived areas had less emergent plants. Tscharntke (1989) showed that reed plants growing in nutrient deprived areas had less BSi, and at the same time more susceptible to gall formation by a gall-making midge, Giraudiella inclusa. In this study, the BSi content was not a response to the presence of the midge, but rather a result of lower Si availability in the growing environment. De Bruyn (1995) suggested a similar mechanism for the gall-forming fly Lipara lucens, indicating that gall-forming species apparently select thin stressed shoots to avoid host–plant resistance.

NUTRIENT STRESS

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

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

Biogeochmochemical implications

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

Carey & Fulweiler (2012) estimated annual uptake of BSi into wetland vegetation at 4.16 Tmole a⁻¹. This was based on an average BSi concentration of 0.62% Si. This average is similar to our average in riverine vegetation (0.46%). The uptake constitutes about 60% of annual riverine transport of Si into the coastal zone and the ocean (Tréguer & De La Rocha 2013). It is unclear whether the estimate in Carey & Fulweiler (2012) includes only emergent species, or also other growth types, but the rough estimate does show that aquatic vegetation forms an important transient sink for Si passing through rivers. Two studies have pointed to a significant presence of phytoliths in swamp soils (Cary et al. 2005; Li, Song & Jiang 2013a), with the carbon occluded in the phytoliths of wetland plant species potentially an important sink to consider in the carbon cycle (Li et al. 2014). It is crucial to understand the recycling rate of Si from plant litter in aquatic ecosystems, and the potential effect of Si on the decomposition rates. Exemplary to this is the strong (permanent) Si sink in the Okavango Delta sediments (Botswana) that can be associated with a dominance of tropical giant grasses such as Cyperus papyrus (Struyf et al. 2015).

The recycling rate of aquatic vegetation-associated BSi is currently understudied. To our knowledge, only experiments on P. australis litter have been performed, and initial field observations in tidal marshes showed rapid recycling of reed phytoliths, with all Si dissolved from the litter within 1 year (Struyf et al. 2007). Data on other species and in other less dynamic environments (tidal marshes receive fresh flood water multiple times during a spring-neap tide cycle) are needed to constrain whether rapid recycling of aquatic vegetation related Si is a rule or an exception.

The spatial pattern of aquatic vegetation also exerts an important effect on patterns of sedimentation and erosion in rivers (Schoelynck et al. 2012a). By slowing down the current, macrophyte patches enhance sedimentation inside and downstream of their canopy. Studies report accumulation of organic matter in macrophyte patches up to 12 times (Sand-Jensen 1998; Cotton et al. 2006), 3–4 times (Kleeberg et al. 2010) and up to six times (Schoelynck et al. 2015) more compared to non-vegetated sediments. It is likely that BSi is also accumulated in the macrophyte patches.

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

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

**SYNTHESIS**

Given the potential importance of Si uptake as a functional trait, and the important biogeochemical consequences Si uptake can have for aquatic and wetland ecosystems, experimental and field studies are needed to further elucidate controls on aquatic plant Si uptake, especially focusing on interactive effects of multiple factors. Such factors can include the abiotic and biotic characteristics suggested above, in experimental set-ups, as current evidence is mostly observational. It should be noted that current research is limited to a small number of species, and a broader phylogenetic coverage would be beneficial. We hope this essay can stimulate the expansion of the research community studying Si cycling in aquatic ecosystems.
vegetation: despite its strong importance for both the plants and the biogeochemical cycle, the number of researchers studying this topic has remained limited.

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Data accessibility

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

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**Supporting Information**

Additional Supporting information may be found in the online version of this article:

**Appendix S1.** Detailed dataset and background information of Fig. 1.