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Silicon affects nutrient content and ratios of wetland plants

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Abstract

Purpose The main objective of this study is to enhance our knowledge about the interplay between the plant Si content and the plant nutrient content as well the nutrient stoichiometry for a broad range of submerged and emergent wetland plants.

Methods We investigated the carbon, nitrogen, phosphorus and silicon content of 16 species (10 submerged and 6 emergent) along a transect within the Biebrza river (Poland) at 10 locations for the years 2006 and 2007. In addition, the relationships between Si and carbon,

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nitrogen and phosphorus content as well as the calculated nutrient ratios (C/N, C/P and N/P) were analyzed.

Results We found evidence for a significant relation of Si to major nutrients (carbon and nitrogen (negative correlation) and phosphorus (positive correlation)) within wetland plants. Our results show that especially submerged plants are able to substitute carbon compound in a significant share by silicon compounds. Nitrogen however is partially substituted by Si for emergent plants. This change in plant nutrient content in turn alters the nutrient stoichiometry of C : N : P.

Conclusion Our data is the first showing a possible important effects of plant Si content on plant nutrition and nutrient cycling in wetlands. Plant Si has to be considered in plant ecology, physiology and biogeochemistry of wetland plants, because of its effects on plant nutrient state. Furthermore, Si may also possibly affect the carbon and nutrient turnover via altered plant nutrient content and subsequently via litter decomposition.

Keywords: carbon substitution; macrophytes; nutrients; stoichiometry; Biebrza; wetland

1 Introduction

A large number of terrestrial plants (i.e. grasses and some trees) and aquatic plants (e.g. emergent, floating leaved and submerged macrophytes) accumulate substantial amounts of silicon (Si) in their tissues (up to ~10 % DW) [1-3]. Silicon in higher plants is taken up as silicic acid (H_4SiO_4) and precipitates usually as phytoliths or the so called silicon double layer in the near epidermis area [2, 4, 5]. In current research the role of Si in plant physiology

commonly neglected the substantial interdependency of Si uptake increasing plant biomass production as well as decreasing the plant nutrient content [2, 6-9]. Silicon has an effect on biomass production of grasses [2, 10], by altering the nutrient stoichiometry and nutrient content of plants [2, 8, 11].

The substitution of a relevant share of plant carbon (C) by Si as suggested by Raven [12] was first proven for a single species experiment using *Phragmites australis* [2]. Another study showed a C substitution by Si for a small number of plants from a broad range of genera from the southern hemisphere [13]. The interplay between C and Si in a broad range of wetland plants (emergent as well as submerged) is less known. Existing data suggests a possible impact of Si accumulation on nutrient content and stoichiometry in wetland plants , but this has still to be elucidated in more detail [2, 9]. The elemental stoichiometry of C, N and P depends on site specific nutrient availability, but strives toward an optimum (max. biomass production) in terms of Redfield's ratio for algae [14]. It is known that Si can impact this stoichiometric optimum (for plants like common reed by increasing nutrient use efficiency) [2].

Wetlands are characterized by biogeochemical cycling of Si, exhibiting strong control on catchment scale Si fluxes [1, 15]. In grass-dominated wetlands in both boreal and tidal environments, a strong impact of plants on source and sink function of wetlands for Si has been highlighted (e.g. [16-20]), with alteration in nutrient availability (eutrophication), human management (e.g. grazing, mowing) and vegetation composition strongly influencing plant Si uptake and recycling of plant BSi. All these studies indicated a near complete biological control on export of fluxes of Si from grass- and/or diatom-dominated wetland systems. Data for non-grass dominated systems are far less available.

The Si cycle is a globally important biogeochemical cycle that directly interacts with major long-term global C sinks [21]. In short, well-established Si-C links are: control by weathering of silicate minerals on atmospheric CO₂ [22], burial of diatom (which have an essential need for Si) carbon in coastal zone and open ocean sediments [23] and direct binding of C within phytoliths (plant Si bodies) of e.g. grasses [24]. Currently it was found that Si is important for net primary production [25] and can also be used to enhance the net CO₂ sink of agricultural ecosystems [26]. Recent research has also shown that Si availability has an impact on the carbon cycle in wetlands due to litter decomposition by affecting litter surface chemistry, nutrient content, nutrient stoichiometry and litter content of carbon compounds [27]. Nutrient content and stoichiometry are important parameters for biomass production and C turnover, whereas stoichiometry reflects the nutrient availability in the soils/sediments and possibly stress levels of the plants [28]. Wetlands play an important role in the regulation of atmospheric CO₂-concentrations [29], because of their immense capacity for C storage via dead organic matter [30]. Hence, examining the impact of Si on plant performance (nutrient content and stoichiometry) is of great interest with regard to global change and carbon turnover. Emergent macrophytes take up C as CO₂ from air and all other nutrients via roots from the soils/sediments, whereas submerged plants have a highly different physiology with a strong nutrient uptake by shoot surface [31, 32]. But less is known how these differences in plant physiology between emergent and submerged plant effects the Si and nutrient content/stoichiometry.

Consequently, the main objective of this study is to enhance our knowledge about the interplay between Si and plant nutrient content and stoichiometry in wetlands. Our hypotheses are that Si will partially substitute plant carbon and will impact plant nutrient content as well as nutrient stoichiometry for a broad range of wetland plants (both emergent and submerged).

2 Material and methods

2.1 Study site and sampling locations

Plant samples were collected along a transect of the Biebrza river located in north-east Poland. A detailed description of the study site and the sampling locations along the river transect are give in Schoelynck et al. [8]. In short: the Biebrza river is ~160 km long and has a catchment area of about 7000 km². As a result of the status of a National Park the low agricultural activities in the catchment result in low nutrient input. The sampling occurred in June 2006 and June 2007 at 10 locations along the Biebrza river. All 10 sites were visited during each year.

2.2 Sampling, sample preparation and analysis

Five individuals of 16 plant species were randomly collected: submerged as well as emergent plants were sampled. Sampled submerged plants (including plants with floating leaved) were: *Ceratophyllum demersum* L., *Hydrocharis morsus-ranae* L., *Myriophyllum spicatum* L., *Nuphar lutea* (L.) Sm., *Potamogeton crispus* L., *Potamogeton lucens* L., *Potamogeton natans* L., *Potamogeton perfoliatus* L. and *Sagittaria sagittifolia* L., whereas the emergent plants are: *Berula erecta* (Huds.) Coville, *Glyceria maxima* (Hartm.) Holmb., *Mentha aquatica* L., *Phalaris arundinacea* L., *Phragmites australis* (Cav.) Trin. ex Steud. and *Rorippa amphibia* (L.) Besser and *Sparganium emersum* Rehmman.

The samples were washed to completely remove attached sediments, algae and macro-invertebrates and subsequently dried at 70 °C to constant weight. The five specimen of each plant were pooled per location, ground and homogenized, resulting in 80 samples of submerged plants and 63 samples of emergent plants. Si was extracted from 25 mg of the plant material by incubation in a 0.1 M NaCO₃ mixture at 80 °C for 4 h [33]. The extracted Si was measured by an ICP-OES (Thermo Fisher, Franklin, MA, USA). This method was proven earlier for correctness [8]. The total phosphorus content was determined according to Walinga et al. [34]. In short: samples were digested with H₂SO₄, salicylic acid and H₂O₂ and subsequently analysed on a colorimetric segmented flow analyzer (SAN⁺⁺, Skalar, Breda, The Netherlands). Carbon and nitrogen measurements were done with an Elementar Vario EL III (Hanau, Germany) elemental analyzer [35]. All chemicals were of analytical grade. The correlation coefficient and significance was calculated by Pearson correlation test.

3 Results

For this sampling campaign no significant differences in Si content of the plant material between the different years (2006 and 2007) and different sampling sites were found (concentrations published in [8]).

We observed an impact of Si on major nutrients (C, N, P) and nutrient ratios (C/N, C/P, N/P). For all species including submerged (80 samples) and emergent (63 samples) plants a negative Pearson correlation of $r = -0.374$ ($p < 0.00005$) was found for Si and C (Fig. 1a). C content ranged between ~20 and 36 mmol g⁻¹ DM⁻¹ and the Si content ranged between 0 and 1.5 mmol g⁻¹ DM⁻¹. We also observed a significant negative relationship between N and Si ($r = -0.242$, $p < 0.005$), with N ranging between ~0.6 and 4 mmol g⁻¹ DM⁻¹ for the analysis of

all species (Fig. 1b). As we observed an effect of Si on N, while no relation between Si and P is apparent, Si has a weak significant negative effect on the N/P ratio (of $r = -0.235$, $p < 0.005$), with a range of N/P ratio's between 5 and 41 (Fig. 1f). No significant correlation was found for Si and P, Si and C/N as well as Si and C/P analyzing all species together.

For submerged plants alone (80 samples) we observed also a strong negative correlation of $r = -0.464$ ($p < 0.0001$) for Si and C (Fig. 2a), with a range of C and Si content similar to the values shown for all plants. But also a positive but weak significant correlation ($r = -0.209$, $p < 0.05$) (Fig. 2c) between P and Si was found. The relationship of C and Si results in a weak negative interdependency of Si content and C/N ratio ($r = -0.236$, $p < 0.05$) and the relationship of both Si to C and P results in negative interdependency of Si to C/P ratio ($r = -0.365$, $p < 0.005$) (Fig. 2d, e). Also a weak significant correlation ($r = -0.216$, $p < 0.05$) between Si and N/P ratios was found (Fig. 2f). For N no significant correlation with Si was found.

A completely different pattern was found for emergent plants (63 samples) (Fig. 3). Si was found to correlate negative significantly with N ($r = -0.374$, $p < 0.005$). This strong relationship of Si and N results consequently in a significant positive weak correlation of Si and C/N ratio ($r = 0.257$, $p < 0.05$) (Fig. 3d). For C, P and both C/P and N/P ratio no significant correlation with Si was found. It should also be noted that some of the significant relationships be partly driven by the sample size of 80 samples for submerged and 63 samples for emergent plants.

4 Discussion

Our Si values are in the typical range as found by other studies [17, 18, 36]. We found an antagonistic correlation of Si and C as well as Si and N for the samples including both emergent and submerged plants (Fig. 1a, b). However, the Si-C correlation is more or less confined to submerged plants (Fig. 2a), whereas the Si-N correlation is attributed to emergent plants (Fig. 3b). For emergent plants the absence of an effect of Si on C may be explained by the homogenous Si content of the plants along the river transect. The C content of emergent plants was observed to be altered, if the Si availability changed within the sediments [2]. Submerged plants however have a different physiology with a strong nutrient uptake by shoot surface [31, 32]. The carbon uptake of submerged plants (predominantly as CO₂) occurs mostly through the leaf surface, but in some cases the uptake via roots is also important [37]. Si uptake however may proceed via both roots and shoots. Si transport within plants is commonly known as driven by transpiration [38], which may in the case of submerged plants be inapplicable, except for plants with floating leaves. Hence, the Si uptake for submerged plants is suggested to occur via the shoot surface. The strong negative correlation between Si and C for submerged plants may be explained by lower C and energy (light) availability of submerged compared with emergent plants [39]. Hence, a substitution of carbon compounds, which have a high energy demand during formation, by Si (which have a low energy requirements for uptake and storage) under low C availability [12] and high Si availability may be beneficial for plant growth of submerged plants. Another important mechanism affecting the C substitution by Si may be the substitution of structural compounds resulting in altered cell wall strength and flexibility, as proposed by Schoelynck et al. [8, 40].

The correlation of N and Si as shown for the whole dataset, possibly due to strong correlation for the emergent plant samples, was previously shown for terrestrial plants (grasses) from China's grasslands [41] and wheat plants [42]. This was explained earlier by a

decrease of Si accumulation under higher N availability [43]. If this effect is based on phylogenetics as both the terrestrial plants of Wallace et al. [43] and some of our emergent plants are grasses, plants with high N demand would accumulate less Si. This suggestion is in line with our findings for emergent plants (Fig. 3b). However, Carey and Fulweiler [19] showed a positive correlation between N availability and Si accumulation. However, their findings may be explained by N fertilization as their experimental setup is possibly resulting in more biomass and thus more stock Si in the aboveground biomass. This in turn results in higher Si cycling, leading to an increase of available Si in the sediments [16].

The effect of Si on the nutrient ratios is, in the case of the C/N-ratio of the submerged plants, an effect of Si on carbon, whereas for the emergent plants it is an effect of Si on nitrogen. The weak but significant effect of Si on the N/P-ratio shown for all plant samples together (emergent and submerged) may be explained by the effect of the submerged plant (Fig. 2f) which showed significant interdependency between Si and N/P-ratios. This may be explained by the (weak) impact of Si on P-accumulation as shown for submerged plants and earlier for common reed [2]. The nutrient content and stoichiometry of plant material is commonly known as one of the factors controlling the decomposition and hence mineralization or sequestration afterwards [44], whereby a stoichiometry similar to the Redfield ratio (i.e. N : P ratio of 16 : 1) [14] leads to faster decay. Also the C : N ratio is described as good indicator for the optimal nutrient supply to the heterotrophic biofilm of the microbial decomposer community [44]. However, recent experiments indicated higher Si content can override this effect, with plant material exposed to high Si availability degrading 90 % faster than controls, even when nutrient-poor [27]. The impact of Si on nutrition of wetland plants is also very important for the nutrient cycling via decomposition of plants material as shown previously [27]. Hence, if the Si availability/cycle is altered as described

earlier [45, 46], then the nutrient turnover and the biogeochemical cycles of wetlands might change, which may also influence the overall litter decomposition process as main part of global C-turnover [47].

5 Conclusion

Altogether, we found evidence for a significant relation of Si to major nutrients as carbon, nitrogen and phosphorus within wetland plants. Our suggested show that especially submerged plants may be able to substitute carbon compounds in a relevant share by silicon compounds, which has a lower energy requirement for uptake and storage compared to carbon compounds [12]. Silicon transport in plant is commonly known to be transpiration driven. For submerged plants this transport is inapplicable due to non-existing water vapor pressure potential gradient within the stomata (except for plants with floating leaves). We therefore suggest that the Si uptake may occur via the surface of the shoots. Also nitrogen may be partially substituted by Si for emergent plants. This in turn alters the nutrient ratios of C : N : P as fundamental measure of nutrient supply, biomass production and litter decomposition afterwards. Hence, plant Si has to be considered in plant ecology, physiology and biogeochemistry of wetland plants, and possible carbon and nutrient turnover via litter decomposition.

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309 Fig. 1: Relationship of silicon to carbon, nitrogen and phosphorus (in mmol g⁻¹ DM⁻¹) as well
 310 as on C/N, C/P and N/P ratios shown for 142 samples of wetland plant species of both
 311 emergent and submerged plants (with an replication of five for each sample of plant
 312 species at every point of the transect).

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Fig. 2: Relationship of silicon to carbon, nitrogen and phosphorus (in mmol g⁻¹ DM⁻¹) as well as on C/N, C/P and N/P ratios shown for 85 samples of submerged plant species (each n=5).

Fig. 3: Relationship of silicon to carbon, nitrogen and phosphorus (in mmol g⁻¹ DM⁻¹) as well as on C/N, C/P and N/P ratios shown for 57 samples of emergent plant species (each n=5).