

Phragmites australis and silica cycling in tidal wetlands

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Received 3 May 2006; received in revised form 23 April 2007; accepted 3 May 2007

Available online 10 May 2007

Abstract

Tidal marshes have recently been shown to be important biogenic Si recycling surfaces at the land–sea interface. The role of vegetation in this recycling process has not yet been quantified. *In situ* and *ex situ* decomposition experiments were conducted with *Phragmites australis* stems. In a freshwater tidal marsh, litterbags were incubated at different elevations and during both winter and summer. Biogenic Si (BSi) dissolution followed a double exponential decay model in the litterbags (from ca. 60 to 15 mg g⁻¹ after 133 days), irrespective of season. Si was removed much faster from the incubated plant material compared to N and C, resulting in steadily decreasing Si/N and Si/C ratios. *Ex situ*, decomposition experiments were conducted in estuarine water, treated with a broad-spectrum antibiotic, and compared to results from untreated incubations. The bacterial influence on the dissolution of dissolved Si (DSi) from *P. australis* stems was negligible. Although the rate constant for dissolved Si dissolution decreased from 0.004 to 0.003 h⁻¹, the eventual amount of BSi dissolved and saturation concentration in the incubation environment were similar in both treatments. *P. australis* contributes to and enhances dissolved Si recycling capacity of tidal marshes: in a reed-dominated small freshwater tidal marsh, more than 40% of DSi export was attributable to reed decomposition. As the relation between tidal marsh surface and secondary production in estuaries has been linked to marsh Si cycling capacity, this provides new insight in the ecological value of the common reed.

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Keywords: Biogenic silica dissolution; *Phragmites australis*; Tidal marsh ecology

1. Introduction

Phragmites australis (common reed) is one of the most widely distributed wetland plant species on Earth. In the tidal environment, it is typically a freshwater species, but its salt tolerance allows it to invade brackish and even marine environments (Soetaert et al., 2004). In many parts of the world, *P. australis* is considered a highly valuable wetland species (Van der Putten, 1997). However, in North America, dense monospecific stands of an invasive non-native genotype (Saltonstall, 2002) have outcompeted other native wetland vegetation types and common reed is often considered an undesirable pest species (Weinstein and Balletto, 1999).

P. australis is highly competitive and produces aboveground biomass typically around 1000 g dry weight m⁻², but reported

values extend as high as 7700 g dry weight m⁻² (Soetaert et al., 2004). *P. australis* is known to have significant ecological and biogeochemical impacts. Nitrogen dynamics in reed dominated tidal wetlands have received a lot of scientific attention (e.g. Windham and Meyerson, 2003; Gribsholt et al., 2005). The sequestration of N in living and dead biomass is high compared to other species. *Phragmites* stands are known to oxidize their rhizosphere with consequences for nutrient cycling, trace element and methane cycling (Sorrell et al., 1997; Van der Nat and Middelburg, 2000).

Despite the substantial scientific attention given to *P. australis* dominated tidal wetlands, Si cycling in these systems has long remained virtually unstudied. Eleuterius and Lanning (1987) have studied Si-dynamics in decomposing *Juncus roemerianus* leaves and reported Si-contents in several other marsh plant species (Lanning and Eleuterius, 1981), while De Bakker et al. (1999) did a study towards the interaction between Si availability and growth of the salt marsh halophyte *Spartina anglica*. Previous studies on *P. australis* litter decomposition have mainly examined rates of mass loss (e.g. Gessner, 2000),

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patterns of microbial respiration (e.g. Kuehn et al., 2004) and changes in nutrient (N, P, K) concentrations (e.g. Mason and Bryant, 1975), and did not consider Si dynamics.

Yet, common reed accumulates large quantities of BSi in its tissue and along the Scheldt tidal freshwater, it was estimated to contain over 90% of all BSi in living freshwater marsh vegetation with above-ground living inventories of 85 g BSi m⁻² (Struyf et al., 2005a). The abundance of Si-rich reed litter on freshwater tidal marsh surfaces has a high potential to contribute to DSi export from tidal marshes. Marshes have recently been shown to be important BSi to DSi recycling surfaces at the land–sea interface (Struyf et al., 2005b, 2006). If DSi dissolution from decomposing reed stems would significantly contribute to the capacity of tidal marshes to buffer DSi concentrations in estuaries during times of DSi limitation, this would shed new light on the ecological importance of reed, now often considered an undesirable pest species in North America.

We have conducted both *in situ* and *ex situ* experiments to quantify the potential contribution of common reed litter to Si cycling in a Scheldt freshwater tidal marsh. *In situ*, litterbags were incubated in winter and summer, to identify possible seasonality in DSi dissolution, and at different marsh elevations, to study if higher flooding frequency enhances the rate of DSi dissolution. Concurrently, total C and N contents of the litter were analyzed, to compare DSi dissolution rates to the loss rates of C and N. During the *ex situ* experiments, antibiotics were added to suppress bacterial activity, in order to understand the influence of bacteria on initial leaching of DSi.

2. Materials and methods

2.1. Study site

In situ incubations were performed in the Tielrode freshwater marsh, situated along the Scheldt estuary (Belgium) (51°06'N, 4°10'E). The Scheldt estuary, located in Northern Belgium (Flanders) and the southwest of the Netherlands, has a history of extensive anthropogenic pollution (Van Damme et al., 2005). A full gradient from salt to fresh tidal is present along the estuary with a large freshwater tidal marsh area. The total surface area of freshwater marshes along the Scheldt is approximately 4,500,000 m² on a total of 30,000,000 m² of tidal marshes. More detailed descriptions of the Scheldt estuary (Struyf et al., 2004; Van Damme et al., 2005) and the Tielrode freshwater marsh (Gribsholt et al., 2005) have recently been published.

2.2. *Ex situ* decomposition experiments

Dead (but standing) *P. australis* stems (length 2–3 m) were collected from the Tielrode freshwater marsh in May 2003. After drying for 30 days at room temperature the reed stems were cut into lengths of approximately 10 cm. Ten replicates of 13 g of (air-dried) reed stem material were then incubated in 2 L of 2.5 μm filtered (to avoid interference by diatom dissolution) Scheldt water at 12 °C in plastic containers. Initial

pH was 7.5. Each replicate included the full length of the stem. Controls without litter were run, and no DSi enrichment was observed in the controls. Reed stems were used because they decompose slower than leaves, contain about 1.5–3 times as much BSi and aboveground shoot biomass is about three to four times aboveground leaf biomass in September, at the height of the growing season (Struyf et al., unpublished data). Shoots therefore represent the major part of the possible DSi source from reed decomposition. A broad-spectrum antibiotic (penicillin-G, streptomycin and neomycin, SIGMA, P3664), an inhibitor of cell-growth for both gram-positive and gram-negative bacteria, was initially added to five replicates at 10 mL L⁻¹ Scheldt water, to suppress bacterial contribution to DSi dissolution. The P3664 addition was repeated every 10 days. P3664 did not suppress fungi, and fungi had strongly developed at the end of the experiment (visual observation).

The initial DSi concentration in the filtered Scheldt water was 0.026 mg Si L⁻¹. DSi concentration in the incubation water was determined after 24 h, 72 h and then approximately every 72 h. Concentrations were corrected for evaporation and used to calculate the amount of DSi released from the incubated reed stems. After 67 days, when an equilibrium concentration (52 ± 2 mg Si L⁻¹, averaged over both treatments) had been reached in the incubations, the water was completely refreshed with newly sampled and filtered (2.5 μm) Scheldt water with an initial DSi concentration of 0.23 mg Si L⁻¹. The difference in DSi concentrations between the refreshing water and initial water was coherent with normal variations of DSi concentrations occurring in the Scheldt estuary in summer (Van Damme et al., 2005).

2.3. *In situ* decomposition experiments

Reed stems were collected from the Tielrode marsh in October 2003. After drying for 30 days at room temperature, the reed stems were cut into equal lengths of approximately 2 cm. Litterbags (1 mm mesh size) were filled with 2 g of air dry stem material. On 12 February 2003, 135 litterbags were incubated in the Tielrode freshwater marsh: 45 were incubated at 5.35 m TAW (TAW = Belgian Ordnance Level, corresponding to the height of mean sea level at low tide), 45 at 5.55 m TAW and 45 at 5.75 m TAW. Flooding frequencies for these elevations were 76%, 65% and 49% of the tides (based on 2002 tidal data), respectively. At each elevation, five litterbags were sampled after 0, 9, 20, 34, 56, 69, 86, 101 and 133 days. A similar experiment was conducted in summer 2004. Here 70 litterbags were incubated on 31 May 2004, at an elevation of 5.35 m TAW (same site as in winter). Ten litterbags were subsequently sampled after 0, 10, 25, 40, 53, 70 and 98 days. Sediment was rinsed from the sampled litterbags; the content was then dried at 80 °C for 48 h. After drying, remaining dry mass was determined and the plant material was grounded with a motor mill and analysed for BSi, N and C content.

Struyf et al. (2005a) observed similar BSi-concentrations in dead standing reed shoots year round in the Tielrode freshwater marsh (major part of the observations between 40 and 60 mg g⁻¹ dry biomass), and much lower BSi-concentrations

in the *P. australis* litter layer (major part of the observations between 15 and 30 mg g⁻¹ dry biomass). This indicated DSi dissolution from the shoots only started after the shoots collapse. Considering the fairly constant BSi concentrations in standing shoots year round, it was preferred to sample shoots for the *ex situ* experiments in winter and summer separately, 1 month before each respective incubation.

2.4. Analysis

To extract biogenic silica, 25 mg of ground, homogenized plant material was incubated for 4 h in 0.1 M Na₂CO₃ at 80 °C (DeMaster, 1981). Extracted dissolved silica was analyzed spectrophotometrically on a Thermo IRIS ICP (Inductively Coupled Plasmaspectrophotometer). Total N and C were analyzed through dynamic flash combustion using a “NC 2100 SOIL” (Carlo Erba Instruments). Computations were implemented using the *stats* package in R freeware (Ihaka and Gentleman, 1996).

3. Results

3.1. Ex situ decomposition experiments

The initial BSi concentration in the incubated reed litter was 60 mg BSi g⁻¹ air dry weight of reed material. The exponential increase in BSi dissolved per gram incubated plant dry weight, fitted well to a first order exponential increase model of the form “ $C_t = C_{\text{sat}}(1 - e^{-kt})$ ”, in which C_t is BSi dissolved at time t , C_{sat} is BSi dissolved at saturation concentration in the incubation water and k is the dissolution rate constant (Bonate, 2005) (Fig. 1). For both models, a highly significant relationship was found between observed and predicted values ($r^2 = 0.97$, $p < 0.0001$ for the model ‘without antibiotics’; $r^2 = 0.98$, $p < 0.0001$ for the model ‘with antibiotics’). Estimates of coefficients b and a , processed to a t -test, were

highly significant in both cases (low standard errors) and estimates were greater for the model ‘without antibiotics’. Dissolved BSi increased exponentially to saturation constants of 9.1 and 8.5 mg BSi g⁻¹ in the control and antibiotic treatment (significantly different, χ^2 -test applied on log-likelihood deviances, $p < 0.0001$). Equilibrium concentrations were 53 ± 1 mg Si L⁻¹ for the control treatments and 52 ± 3 mg Si L⁻¹ for the antibiotic treatment. The dissolution rate constant was significantly higher (χ^2 applied on log-likelihood deviances, $p < 0.0001$) in the control than in the antibiotic treatments (0.004 and 0.003 h⁻¹, respectively). The first order exponential increase models fitted on the pre-refreshing data also describe the temporal evolution of non-antibiotic and antibiotic experiment after refreshing of the incubation water without tuning the parameters (Fig. 1).

3.2. In situ decomposition experiments

3.2.1. Silica

BSi content decreased rapidly in the incubated litterbags during both winter and summer experiments. No consistent increase or decrease of the rate or extent of BSi dissolution with flooding frequency was observed (Fig. 2a). Observed BSi dissolution during the winter experiment was highest at the intermediate flooding frequency (555 cm TAW) and lowest at the highest flooding frequency (535 cm TAW) (variance analysis with time and elevation as sorting variables, elevation effect $F_{2,119} = 62.003$, $p < 0.001$, Scheffe post hoc test for elevation, $555 < 575 < 535$). There was thus no consistent decrease or increase of DSi release from the litterbags with decreasing flooding frequency. The decrease in BSi concentration in the litterbags averaged for all flooding frequencies (15 replicates every time step) was fitted by a composite exponential decay model (Fig. 2b) of the form “ $B_t = (B_0 - B_1)e^{(-Rt)} + B_1e^{(-Lt)}$ ”, in which B_t is the BSi concentration at time t , B_0 is the initial BSi

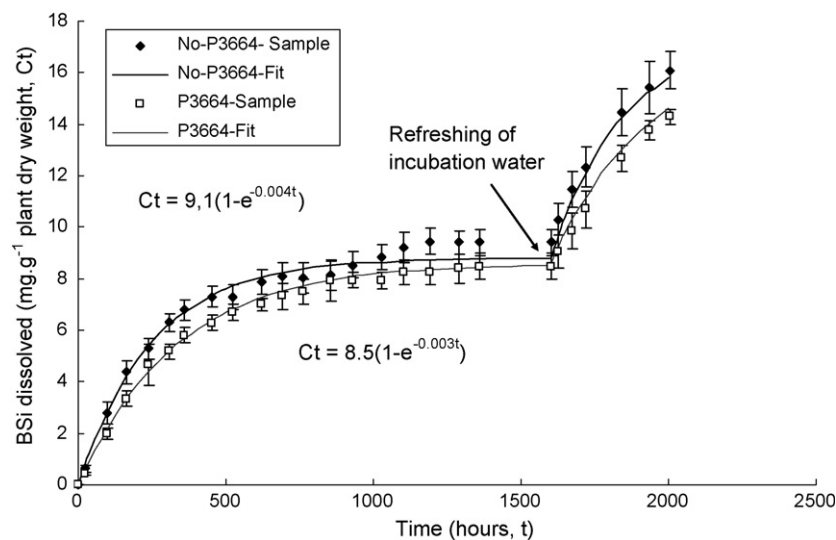


Fig. 1. Average BSi ($n = 5$) dissolved from *Phragmites australis* stems during *ex situ* incubation experiments in Scheldt water. P3664-samples were treated with the broad-spectrum antibiotic P3664. Initial DSi incubation concentration was 0.026 mg Si L⁻¹. After refreshing of incubation water, DSi concentration was reduced again to 0.23 mg Si L⁻¹ (error bars = standard deviation).

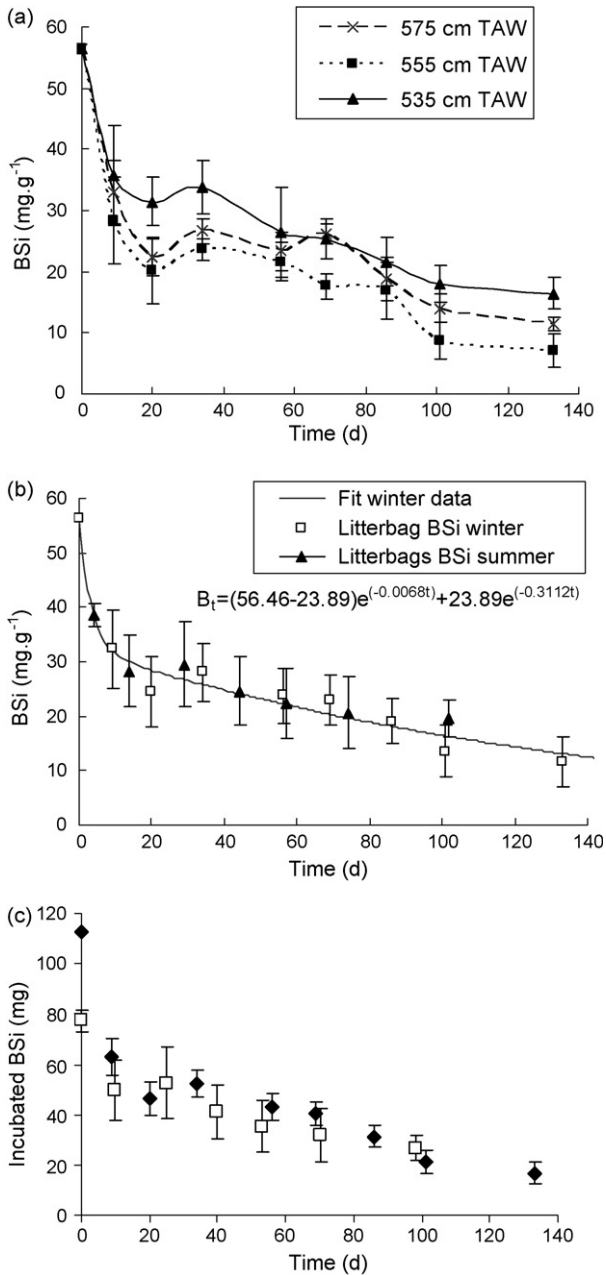


Fig. 2. *P. australis* during *in situ* decomposition experiments. (a) The average ($n=5$) decrease in BSi concentration in litterbags incubated at different elevations (TAW = height above mean low sea level) in winter 2003–2004. (b) Comparison of average decrease in BSi concentration in litterbags in summer 2004 ($n=10$) and winter ($n=15$). The double exponential model was fitted to the winter data. (c) The remaining total incubated BSi in the litterbags (error bars = standard deviation).

concentration at incubation, B_1 is the non-refractory portion of BSi and L and R are rate constants for respectively the initial fast BSi dissolution and the subsequent slow BSi dissolution.

To test potential seasonality in BSi dissolution, the litterbag experiment was repeated at one marsh elevation in summer (5.35 m TAW). Initial concentration of BSi in the litterbags was much lower in summer compared to winter (56 mg g⁻¹ versus 39 mg g⁻¹). This could be the result of random variation of Si

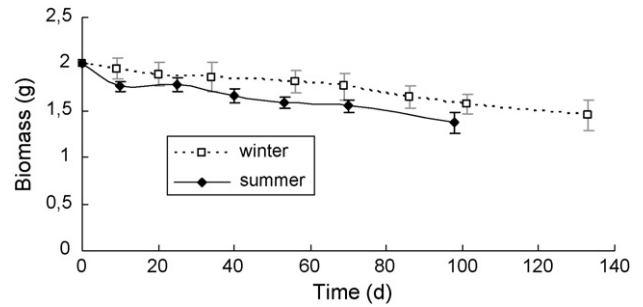


Fig. 3. Average ($n=5$) biomass decrease in *P. australis* stems incubated in summer and winter 2003–2004 (error bars = standard deviation).

content of reed shoots sampled for summer and winter experiments. To be able to compare BSi dissolution from winter and summer shoots, the incubation time for the summer litterbags was set from day 0 to day 4. At day 4, the winter litterbags had an average BSi content of 39 mg g⁻¹. After this correction, the summer litterbag data are fitted by the composite exponential decrease model observed in winter (Fig. 2b). The model observed in both winter and summer suggests that over 98% of BSi in reed litterfall is recycled to DSi in 1 year (Fig. 2c). At 150 days after deposition on the marsh floor, only about 15% of the BSi has not yet been released from the reed shoots.

3.2.2. Biomass, nitrogen and carbon

Average biomass in the incubated litterbags decreased slightly faster in summer than winter (Fig. 3). In winter, initial C concentrations in the incubated litter were lower than in summer, while N concentrations were initially higher in winter (Fig. 4a and b). N concentrations doubled in summer and remained constant in winter. C concentrations were between 346 and 415 mg g⁻¹ during the complete incubation period in both winter and summer. Si dissolved much faster compared to N and C, and Si/N and Si/C ratios (mg Si [g biomass]⁻¹/mg (N or C) [g biomass]⁻¹) rapidly decreased during the decomposition process (Fig. 4c and d). There was an increase in C/N ratio (mg C [g biomass]⁻¹/mg N [g biomass]⁻¹) in both winter (from 45 to 63) and summer (from 72 to 94) in the initial 10 days of incubation. Afterwards, the C/N ratio remained constant at around 60 in winter, while it decreased from 94 to 40 in summer (not shown).

4. Discussion

Although initial Si dissolution rate was lower in the experiments treated with antibiotics, there was almost no influence on eventual turnover time of reed BSi. This contrasts with studies on diatom BSi dissolution, which is strongly enhanced by bacterial activity (Patrick and Holding, 1985; Bidle and Azam, 1999). In our litterbag results, BSi dissolution was according to a composite exponential decay model; diatom derived biogenic silica dissolution in equatorial Pacific sediments also followed a two-component model (Hammond et al., 1996). No data were found for *P. australis* (or any other marsh grass) litter.

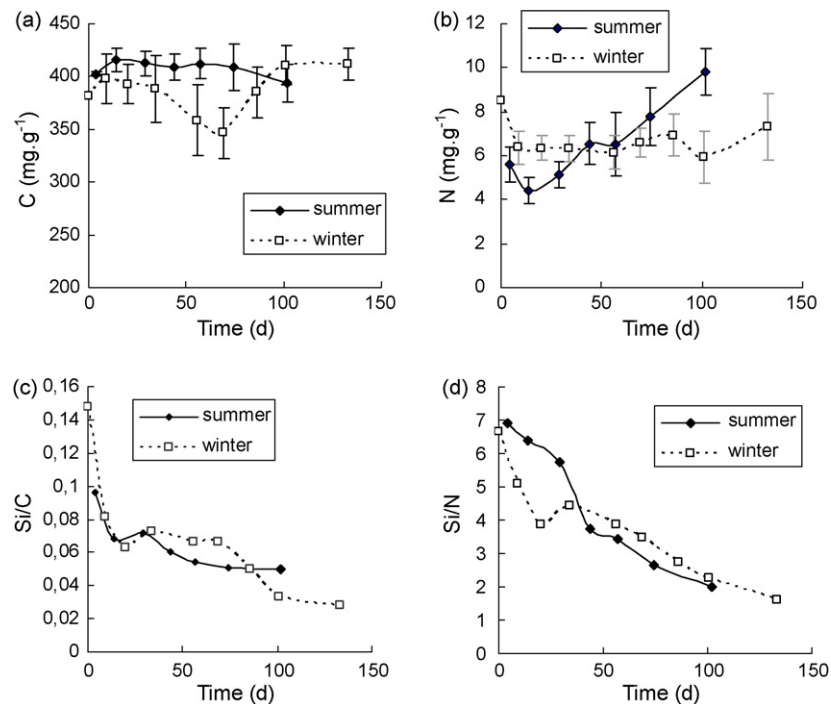


Fig. 4. Carbon (a) and nitrogen (b) content in *P. australis* stems in litterbags incubated in summer and winter (error bars = standard deviation). Mean Si/C [(mg g⁻¹)/(mg g⁻¹)] ratio (c) and Si/N [(mg g⁻¹)/(mg g⁻¹)] ratio (d) in the incubated litterbags.

In contrast to other studies on *P. australis* decomposition, biomass started to decrease from the first day on; this could be attributed to our cutting of shoots into small pieces. Fungi, highly abundant on *P. australis* along the Scheldt (Van Ryckeghem and Verbeke, 2005) are probably an important factor. A 6-month delay was observed before biomass decrease started in full length collapsed reed shoots (Gessner, 2000; Van Ryckeghem et al., 2006). Full-length shoots have relatively few surfaces where fungi can penetrate the inner plant tissue, as opposed to cut pieces.

Our litterbag results are not evidence that the decrease in BSi concentrations is attributed to phytolith dissolution. Phytolith burial after litter decay is another possibility, but several indications point out that the BSi is dissolved. The BSi *ex situ* experiments was rapidly dissolved (in 7 days a concentration of 20 mg Si L⁻¹ was found in the incubators, and 4 mg BSi was dissolved per gram incubated plant material). The rapid dissolution observed in the marsh (85% of the BSi after 150 days), can be explained at similar dissolution rates. The marsh is year round inundated with tidal water with DSi concentrations below 10 mg Si L⁻¹ (Struyf et al., 2005b) and DSi concentrations in the porewater are 15 mg Si L⁻¹ or less (Struyf et al., 2005a). The driving force for DSi dissolution from the litter is continuously high. Secondly, the ratio of diatom shells to phytoliths in the marsh sediment is 6 to 1, suggesting that the high BSi content of the sediment is mainly originating from diatom deposition (Struyf, unpublished).

Dissolution of BSi showed no consistent relation with flooding frequency. This may indicate that the main part of the BSi is released into marsh soil and puddle water between tidal flooding events. This idea of predominant release to soil water

rather than tidal bulk water during inundation is consistent with previous observations that almost all export of DSi from the studied freshwater marsh occurred during the seepage water phase (Struyf et al., 2005a,b, 2006). The seepage water is a mixture of flood water and soil and puddle, slowly flowing out of the marsh between two tidal floodings. Water level at that moment is several meters below the marsh elevation level in the main estuarine channel (5–6 m), and gravitation causes the seepage water to be released from the sediments to the creeks (Struyf et al., 2006).

Si was removed from the decomposing plant litter much faster than N and C, resulting in steadily decreasing Si/(C, N) ratios. This contrasts with observations by Eleuterius and Lanning (1987), who observed continuously increasing Si content in decomposing *J. roemerianus* leaves. Decomposition in the *Juncus* study was in standing dead leaves, mainly by saprophytic fungi. Si was removed from the *J. roemerianus* leaves only after collapse, as opposed to N and C, which were already removed in the standing leaves. Similar processes could cause the high Si content (>5% of dry weight) observed in standing dead reed stems (Struyf et al., 2005a). The relative increase in N content in the decomposing litter added to the decreasing Si/N ratio.

The fast dissolution of DSi from decomposing reed litter adds to the DSi recycling capacity of tidal marshes. Tidal marshes import BSi and export DSi, though with some delay (Struyf et al., 2006). During summer months, export of DSi from marshes along the Scheldt tidal freshwater estuary was estimated to approach that supplied by the river Scheldt (Struyf et al., 2006). Sediment BSi is recycled slowly. After approximately 30 years, 60% of the BSi in a mature (=elevation

approximately in equilibrium with the mean high water level) Scheldt freshwater marsh has been recycled to DSi (Struyf et al., 2007). In comparison, the BSi recycling from the *P. australis* vegetation observed in this study is much faster. The reed vegetation in tidal areas is highly dynamic; at peak biomass (September), 20% of the standing *P. australis* stems in reed dominated vegetation were dead (May 2004: 1872 shoots counted in 24 plots of 1 m²). This indicates that approximately 80% of the shoots from the previous growing season had collapsed. A BSi stock study in the Tielrode freshwater marsh indicated that vegetation in the 3500 m² area contained approximately 115 kg, 111 of which were attributable to *P. australis* (0.09 kg BSi m⁻², in *Phragmites* stands) (Struyf et al., 2005a). A large part of the BSi could be recycled in 1 year, due to the highly dynamic character of the vegetation and high DSi dissolution rate from decomposing *P. australis* stems. Although BSi content in the *P. australis* vegetation in the studied freshwater marsh was low compared to sediment BSi content (approximately 5300 kg in the upper 30 cm for the full 3500 m² or 1.5 kg m⁻²) (Struyf et al., 2005a), yearly release of DSi from the sediment was modeled (Struyf et al., 2007) to be lower, namely 0.04 kg m⁻².

P. australis stands thus clearly have the potential to actively enhance the storage and recycling capacity of tidal marshes in estuarine Si cycling. Through DSi recycling, *P. australis* dominated tidal marshes could enhance the resilience of coastal systems to eutrophication, often characterized by a shortage of Si compared to available N and P.

This adds new insight in the ecological value of *P. australis*, often considered an undesirable pest species in the USA (Weinstein and Balletto, 1999). Few marsh plant species have been studied for their Si-dynamics; still arguments exist for a possible increase in Si buffering capacity in *P. australis* dominated marshes. *J. roemerianus* (Eleuterius and Lanning, 1987) and *Spartina anglica* (De Bakker et al., 1999) both have considerably lower BSi concentration (below 10 and 12 mg g⁻¹ respectively in living plants) (Lanning and Eleuterius, 1981). In *J. roemerianus*, this value rose to 25 mg g⁻¹ in dead standing plants. *P. australis* however contains up to 60 mg g⁻¹ in dead plants (Struyf et al., 2005a) and is known for its vast biomass and extensive litter layer (Rooth et al., 2003). On the other hand, *Scirpus validus* and *Distichlis spicata* have reported BSi-content values of up to 34 and 45 mg g⁻¹, respectively (Lanning and Eleuterius, 1981); other marsh plants might thus function similarly to *P. australis* in the coastal Si biogeochemistry. However, research is as of yet too scarce to provide general insight in the role of marsh plants in the estuarine silica biogeochemistry, and experiments in other systems would provide valuable comparison material.

We conclude that although *P. australis* vegetation comprises only a small stock of BSi in tidal marshes in comparison to sediment, it is a far more rapidly recyclable sink. Moreover, DSi recycling from reed litter in tidal marshes is almost 100%, as opposed to sediment, where around 40% of imported BSi is buried and becomes unavailable for recycling (Struyf et al., 2007). *P. australis* actively enhances Si cycling in tidal environments, and this could be essential in its dominance in

the system, through the beneficial effects of Si fixation in plant tissue (Epstein, 1999).

On a broader scale, beyond coastal biogeochemistry, common reed is one of the most widely distributed plant species on Earth. It is present worldwide in a wide range of wetlands. In the tidal environment, rapid recycling is probably the result of the dynamic character of the marsh systems: frequent flooding and efficient drainage stimulates rapid recycling of reed BSi. In other wetlands systems, with less frequent flooding and/or less efficient drainage, *Phragmites* BSi is more likely to be buried after plant collapse. The high biomass which characterizes the reed, combined with its ubiquitous distribution, make it an as of yet unrecognized, yet important factor in the global biogeochemical cycling of Si. In the light of this observation, the role of *P. australis*, and marsh plants in general, in the Si cycle deserves more attention than it has currently received.

Acknowledgements

L. Clement and E. De Bruyn analyzed samples in the “UA, University of Antwerp, Department of Biology, Testing Laboratory for Chemical Water Quality”. Special thanks to IWT (Institute for Promotion of Innovation through Science and Technology, Flanders) for scientific project funding (project number 13263 “The role of freshwater marshes in the estuarine silica cycle”), to FWO (Fund for Scientific Research, Flanders) for funding the “Scientific Research Community” project “Ecological characterization of European estuaries, with emphasis on the Scheldt estuary” and to FWO-NWO (Fund for Scientific research, Flanders, The Netherlands) for funding project number 832.11.004 (“The role of freshwater marshes in the retention and transformation of nitrogen in estuaries, a whole ecosystem labeling study”). Thanks to Hans Backx and one anonymous reviewer for their constructive comments. Eric Struyf is thankful for personal finance by EU Marie-Curie Programme and FWO. This is NIOO publication number 4049.

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