Tracing Si–N–P ecosystem-pathways: is relative uptake in riparian vegetation influenced by soil waterlogging, mowing management and species diversity?

Eric Struyf · Wiktor Kotowski · Sander Jacobs ·
Stefan Van Damme · Kris Bal · Wout Opdekamp ·
Hans Backx · Dimitri Van Pelt · Patrick Meire

Published online: 18 May 2011

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Abstract Despite the growing concern about the importance of silicon (Si) in controlling ecological processes in aquatic ecosystems, little is known about its processing in riparian vegetation, especially compared to nitrogen (N) and phosphorus (P). We present experimental evidence that relative plant uptake of N and P compared to Si in riparian vegetation is dependent on mowing practices, water-logging and species composition. Results are obtained from a controlled and replicated mesocosm experiment, with a full-factorial design of soil water logging and mowing management. In our experiments, the Si excluding species *Plantago lanceolata* was dominant in the mown and non-waterlogged treatments, while Si

accumulating meadow grasses and *Phalaris arundinacea* dominated the waterlogged treatments. Although species composition, management and soil moisture interacted strongly in their effect on relative Si:N and Si:P uptake ratios, the uptake of N to P remained virtually unchanged over the different treatments. Our study sheds new light on the impact of riparian wetland ecosystems on nutrient transport to rivers. It indicates that it is essential to include Si in future studies of the impact of riparian vegetation on nutrient transport, as these are often implemented as a measure to moderate excessive N and P inputs.

Keywords Riparian meadows · Riparian wetlands · Silicon · Nitrogen · Phosphorus · Vegetation · Eutrophication

Guest editors: Dominik Zak, Robert McInnes, Jörg Gelbrecht / Restoration, biogeochemistry and ecological services of wetlands

Electronic supplementary material The online version of this article (doi:10.1007/s10750-011-0737-x) contains supplementary material, which is available to authorized users.

E. Struyf · S. Jacobs · S. Van Damme ·
K. Bal · W. Opdekamp · H. Backx · D. Van Pelt ·
P. Meire
Department of Biology, Ecosystem Management
Research Group, University of Antwerp,
Universiteitsplein 1C, B2610 Wilrijk, Antwerp, Belgium

W. Kotowski (✉)
Department of Plant Ecology and Environmental
Conservation, University of Warsaw, Warsaw, Poland
e-mail: w.kotowski@uw.edu.pl

Introduction

The uptake, storage and recycling of silicon (Si) in ecosystem biomass and soils are now recognized as important components of silicon transport through the terrestrial environment (Conley, 2002; Derry et al., 2005; Street-Perrott & Barker, 2008; Struyf & Conley, 2009), but the relative importance of the biological buffer in different ecosystems, and the impact of environmental forcing factors on the efficiency of storage, uptake and recycling still remains poorly quantified. Si is a key nutrient in determining the species composition of aquatic and coastal

phytoplankton communities (Cloern, 2001). The commonly observed effect of increased anthropogenic inputs of nitrogen (N) and phosphorus (P) to aquatic ecosystems is a shift in the coastal phytoplankton community to one dominated by dinoflagellates (Lotze et al., 2006), caused by dissolved Si (DSi) limitation of diatoms (Conley et al., 1993). A lack of DSi can lead to a less efficient food web structure as well as to hypoxia and harmful blooms of toxic algae (e.g. Anderson et al., 2002). Silicon also plays an essential role in the global carbon (C) cycle. A continuous import of Si from the terrestrial environment is necessary to maintain the biological C pump in the ocean (Tréguer & Pondaven, 2000), and mineral weathering of silicate minerals is one of the major terrestrial sinks for carbon dioxide (CO₂) (Berner, 1992). The poor quantification of the biological Si buffer in ecosystems forms a prime challenge in constraining the silicon cycle related C sinks.

Wetlands and meadows are prime candidates to form a hot-spot in the biological Si buffer, as they can accumulate large amounts of biogenic amorphous Si (ASi) (Blecker et al., 2006; Struyf & Conley, 2009) in the form of plant phytoliths, diatoms and sponge spicules. Riparian meadows are well-established buffers in the N and P cycle. They affect the output of these nutrients to rivers through permanent or temporary uptake in vegetation, detritus and soils and through transformation processes, e.g. removal by denitrification (e.g. Güsewell, 2005; Olde Venterink et al., 2006). Riparian wetlands are often (re)established as a countermeasure against excessive N and P export from agricultural catchments. Up to now however, little research has focused on the influence of ecosystem characteristics on Si processing in riparian meadows or wetlands. Management has been observed to potentially interfere with the storage of ASi near the surface of riparian wetlands (Struyf et al., 2009), but experimental evidence is currently lacking (Struyf & Conley, 2009).

We analyzed uptake of Si by riparian vegetation in reference to N and P in mesocosm communities grown for one season under contrasting moisture and management conditions. Earlier experiments have focused on N, P and often K and C, while failing to include Si. Our study sheds new light on the impact of riparian wetland ecosystems on nutrient transport to rivers, and is new evidence of the importance of the role of vegetation in terrestrial Si fluxes.

Materials and methods

Mesocosms

We established a full-factorial mesocosm experiment with soil water-logging and summer mowing as factors, each of them in two levels (waterlogged, anoxic vs. non-waterlogged, oxic and mown vs. unmown). The experimental set-up is described in Kotowski et al. (2010). Briefly, mesocosms were composed of PVC containers of 91 × 111 cm surface and 61 cm height. Outflow taps located at the bottom of side walls connected to PVC pipes allowed for the control of the water level. Containers were filled with 20 cm of drainage substrate (Argex clay aggregate, Argex NV, Zwijndrecht, Belgium) separated by geo-textile from a 30 cm cover of a soil mixture containing 3:1 volumetric parts of fen peat and alluvial clay. Mixing fen peat and clay ensured that the soil would have high water potential and mineral content (clay) and at the same time, high organic matter content (peat) necessary to produce reduced conditions after water-logging. Presence of peat in the soil also allowed for easier percolation of water under non-water logged conditions. To maintain eutrophic conditions throughout the experiment, an initial amount of 168 g N, 192 g P, 216 g potassium (K) and 24 g magnesium (Mg) per m³ soil in an easily soluble form (PG-mix Floranid, COMPO Benelux nv, Deinze, Belgium), and a slow release fertilizer (6 months release time; Osmocote, SCOTTS Professional, Sint-Niklaas, Belgium) containing 300 g N, 180 g P and 180 g K per m³ soil were added. These values are at the upper limit of annual nutrient input in European floodplains (Olde Venterink et al., 2006).

Forty mesocosms were placed in a block of 4 × 10. Water was supplied by sprinklers installed 30 cm above each container once (spring, autumn) or twice (summer) a day. Watering time depended on the time of the year (between 5 and 25 min per day) and specifically ensured that plants were not limited by water shortage. Excessive water could flow out of the system through the outflow pipe. In anoxic soils, the water level was held constant at 2–5 cm below soil surface, while the outflow was levelled at the bottom of the containers in the oxic soils.

The species used in the experiment were typical of Central European floodplains. We carefully selected

species as to have a similar representation of typical fen, wet meadow and mesic meadow species and to assure that each of these groups contained species from various functional types and growth forms (Supplementary material). A seed mixture of 37 species was introduced on the 15th of May 2006 in a density of approximately $1,000 \text{ seeds m}^{-2} \text{ species}^{-1}$. Soil moisture measurements at 5 cm depth carried out in mid June between two watering treatments confirmed differences between the waterlogged and the non-waterlogged treatments (soil moisture: $54.2\% \pm 12.1$ and $32.4\% \pm 3.5$, respectively, by weight, t test $P < 0.001$).

Sampling

The above-ground biomass of the 20 mesocosms subjected to the summer mowing treatment was harvested at the end of June 2006. Biomass was sorted to species level, except for the meadow grasses which were grouped. Dry biomass of all species was determined separately (except for the meadow grasses) in each mesocosm after 72 h of drying at 70°C . At the end of the experiment (September 2006), the above-ground biomass of all 40 mesocosms was harvested and the sorting and drying was carried out as described above.

Nutrient analysis

N, P and Si concentrations in plant biomass for all established species were determined. If a species established in more than seven mesocosms with the same combination of mowing and aeration treatment, seven randomly chosen replicates were analyzed for their N, P and Si content.

After drying, the plant material was grounded with a motor mill and analyzed for N, P and Si content. ASi content was analyzed through incubation of 25 mg of ground, homogenized plant material for 4 h in $0.1 \text{ M Na}_2\text{CO}_3$ at 80°C (DeMaster, 1981). Extracted dissolved silicon was subsequently analyzed spectrophotometrically on a Thermo IRIS ICP (Inductively Coupled Plasmaspectrophotometer). N and P content were analyzed according to Walinga et al. (1989) on a colorimetric segmented flow analyzer.

Nutrient uptake at the vegetation level

To allow the analysis of nutrient uptake at community level during the experiment (May–September 2006), the dry weight of every species was multiplied with the average N, P and Si content observed for the species in a certain treatment. The total N, P and Si uptake in biomass for every mesocosm was then calculated by summation of the calculated total nutrient uptake in all species. For the mown treatments, this is the summation of the May–June and July–September uptake.

Statistical analyses

A one-way ANOVA analysis was used to comparing the treatments for different variables (Biomass, N, P and Si uptake, N:P ratio, N:Si and P:Si). Classification of the treatments was performed with Post-hoc Scheffe tests. All analyses were performed in SPSS (Statistical Package for the Social Sciences) 14.0 (SPSS, 2005).

Results

Vegetation patterns and biomass

In total, 26 species established in the mesocosms but only 14 were present in sufficient amounts to allow for chemical analyses (see Kotowski et al., 2010 for detailed information on species recruitment in each treatment). Three meadow grasses established (i.e. *Lolium perenne* L., *Poa pratensis* L., and *Alopecurus pratensis* L.): these were grouped as one taxon within the analysis. Another grass species, *Phalaris arundinacea* L. was considered separately, as it is a typical wetland grass, while the other grouped species are typical meadow grasses. As such, 11 species and one group-taxon were included in the analysis: “meadow grasses (*L. perenne*, *P. pratensis* and *A. pratensis*)”, *Achillea millefolium* L., *Centaurea jacea* L., *Cirsium oleraceum* L. Scop., *Daucus carota* L., *Epilobium hirsutum* L., *Leontodon autumnalis* L., *Lycopus europaeus* L., *Lythrum salicaria* L., *P. arundinacea*, *Plantago lanceolata* L. and *Valeriana officinalis* L..

Table 1 Results for a one-way Anova analysis comparing the four treatments for different variables: biomass, nitrogen (N), phosphorus (P), silicon (Si) uptake, and weight ratios of N:P, N:Si and P:Si

Variable	<i>F</i> value and <i>P</i> value	Effect
Total biomass		
Biomass	$F_{3,39} = 26.46; P < 0.001$	ONM = OM > AM = ANM
N uptake	$F_{3,39} = 60.504; P < 0.001$	OM > ONM > AM = ANM
P uptake	$F_{3,39} = 45.90; P < 0.001$	OM > ONM > AM = ANM
Si uptake	$F_{3,39} = 18.77; P < 0.001$	ONM = OM > AM = ANM
N:P ratio	$F_{3,39} = 140.963; P < 0.001$	OM > ONM > AM > ANM
N:Si ratio	$F_{3,39} = 15.826; P < 0.001$	AM = OM > ONM = ANM
P:Si ratio	$F_{3,39} = 13.674; P < 0.001$	AM = OM > ONM = ANM
Without <i>Plantago</i>		
Biomass	$F_{3,39} = 3.107; P < 0.04$	ONM = OM = AM = ANM
N uptake	$F_{3,39} = 1.45; P > 0.2$	ONM = OM = AM = ANM
P uptake	$F_{3,39} = 1.30; P > 0.2$	ONM = OM = AM = ANM
Si uptake	$F_{3,39} = 12.84; P < 0.001$	ONM = OM > AM = ANM
N:P ratio	$F_{3,39} = 30.076; P < 0.001$	OM > ONM = AM = ANM
N:Si ratio	$F_{3,39} = 75.126; P < 0.001$	AM > ANM > OM = ONM
P:Si ratio	$F_{3,39} = 78.514; P < 0.001$	AM > ANM > OM = ONM

The result for the full Anova test is shown (*P* value for significance, *F* value as the critical value extracted from the *f*-distribution with 3 and 39 degrees of freedom), as well as the classification of the treatments according to Post-hoc Scheffe tests (*OM* oxie, mown; *ONM* oxie, unmown; *AM* anoxic, mown; *ANM* anoxic, unmown). The analysis was repeated for the full vegetation, and for vegetation excluding *Plantago lanceolata*, the main silicon excluder in the analysis

The total above-ground biomass was higher in the non-waterlogged, oxie treatments (Table 1). Biomass in oxie treatments was dominated by *P. lanceolata*, and to a lesser extent, by *P. arundinacea*, *D. carota* and *A. millefolium* (Fig. 1). Biomass in the waterlogged, anoxic treatments was dominated by meadow grasses and *P. lanceolata*, and to a lesser extent by *P. arundinacea* (Fig. 1). A clear shift of the dominant species was apparent between anoxic and oxie treatments, with meadow grasses dominating the anoxic treatments and *P. lanceolata* the oxie treatments (Fig. 1). More than 80% of the decrease in total biomass under anoxic conditions could be attributed to *P. lanceolata*, with a strong decline in biomass, both in mown ($-1,000 \text{ g dry weight m}^{-2}$ of *P. lanceolata* biomass on average) and unmown mesocosms ($-1,360 \text{ g dry weight m}^{-2}$ on average). Given the importance of *P. lanceolata* for total biomass production, we also tested for differences in biomass excluding *P. lanceolata*. Although a marginally significant effect of treatment on biomass without *P. lanceolata* biomass existed ($P < 0.04$), the post-hoc Scheffe tests did not separate any of the treatments individually (Table 1).

Nutrient concentrations at the species level

The plant nutrient concentration among the different replicates only showed small variability (Table 2). Results for nutrient contents will focus on the main dominant species *D. carota*, *A. millefolium*, “meadow grasses”, *P. arundinacea* and *P. lanceolata*, which represented over 90% of nutrient uptake. Average biomass for the dominant species, and average N, P and Si concentrations in the plant tissue is summarized in Table 2. *P. lanceolata* and *D. carota* had low N, P and Si contents compared to the other dominant species. The species in the anoxic treatment generally contained less N, P and Si compared to the oxie treatments. Highest relative differences were observed for Si content in *P. arundinacea*, meadow grasses and *A. millefolium*, which had more than twice the relative Si content in oxie compared to anoxic treatments.

Nutrient uptake

Total uptake of nutrients (N, P and Si) in the oxie treatments was high compared to anoxic treatments

Fig. 1 Contribution of different species to total biomass in the different treatments (averaged, $n = 10$ for every treatment)

(Fig. 2; Table 1). Under oxic circumstances, N and P uptake were higher in the mown treatments; this effect was not apparent for Si uptake (Table 1). The differences for N and P uptake were attributable to *P. lanceolata* biomass. Excluding this, no differences in total N and P uptake were apparent (Table 1, Fig. 2 lower panel). This was not the case for Si uptake; excluding *P. lanceolata* biomass had no effect on Si uptake (Table 1; Fig. 2) as there is almost no Si in *P. lanceolata* (Table 2).

In mown treatments more N and P were taken up compared to Si than in unmown treatments, both under oxic and anoxic conditions (Fig. 3; Table 1). The relative uptake of Si dropped mainly as a result of increasing *P. lanceolata* abundance in the mown treatments (N:Si ratio in *P. lanceolata* ranged between 17 and 38, while, e.g. *P. arundinacea* N:Si ranged between 2 and 5). Although significant differences existed in N:P ratio across the treatments (Table 1), these differences were very small (Fig. 3).

If we remove *P. lanceolata* from the analysis, all remaining dominant vegetation consists of Si accumulators. This had little effect on N:P ratio in the vegetation across the treatments (Fig. 3; Table 2), although small significant differences still existed (Table 2). Removing *P. lanceolata* from the analysis had almost no effect on the total Si content of plants, while the N and P taken up by the vegetation decreased drastically (Fig. 2). The N:Si and P:Si ratio in the Si accumulator (non-*Plantago*) biomass was mainly related to the water-logging in the soil (Table 1, Fig. 3), although mowing had a significant effect in the anoxic treatments (Table 1).

In summary, the N:P ratio only differed marginally over species composition, soil moisture and mowing conditions. In contrast, the ratio at which Si was taken up relative to the other nutrients was significantly different. Mowing enhanced occurrence of *P. lanceolata*, and as such decreased relative uptake of Si. In the accumulator biomass, relative uptake of Si to N and P was mainly related to water logging.

Table 2 Biomass (BM), silicon (Si), nitrogen (N) and phosphorus (P) contents for all dominant species, sampled in June (first mowing) and September (definitive sampling)

	Treatment																			
	Oxic, unmown					Oxic, mown					Anoxic, unmown					Anoxic, mown				
September	BM	SE	Si	SE	<i>n</i>	BM	SE	Si	SE	<i>n</i>	BM	SE	Si	SE	<i>n</i>	BM	SE	Si	SE	<i>n</i>
Meadow grasses	97	23	8.6	1.3	7	37	22	6.6	0.7	7	575	20	3.3	0.2	7	160	28	3.0	0.1	7
<i>Achillea millefolium</i>	267	40	7.9	0.9	7	18	4	10.2	1.7	6	7	1	4.0	0.5	6	3	1	3.2	0.4	3
<i>Daucus carota</i>	227	48	1.9	0.9	7	81	21	0.9	0.4	7	16	1	0.5	0.1	7	18	9	0.7	0.4	7
<i>Phalraia arundinacea</i>	378	72	10.7	1.5	7	195	41	9.8	2.3	7	245	43	4.3	0.6	7	143	32	4.7	2.4	7
<i>Plantago lanceolata</i>	1090	48	0.9	0.2	6	760	88	0.5	0.1	7	157	31	0.5	0.1	6	229	80	0.5	0.1	7
June	N	SE	P	SE	<i>n</i>	N	SE	P	SE	<i>n</i>	N	SE	P	SE	<i>n</i>	N	SE	P	SE	<i>n</i>
Meadow grasses	19.0	0.8	3.7	0.1	7	23.3	2.8	5.1	0.2	7	14.7	0.6	3.2	0.2	7	18.5	2.0	3.9	0.4	7
<i>Achillea millefolium</i>	19.5	1.6	3.8	0.3	7	22.2	2.0	4.5	0.4	6	14.1	0.6	2.7	0.1	6	20.5	0.9	3.6	0.2	3
<i>Daucus carota</i>	14.3	1.6	3.4	0.4	7	19.3	1.5	4.1	0.3	7	12.9	0.5	3.1	0.2	7	15.0	2.1	3.2	0.2	7
<i>Phalraia arundinacea</i>	18.3	0.6	3.8	0.2	7	20.3	2.0	3.9	0.4	7	9.5	0.9	2.0	0.2	7	15.3	4.0	2.7	0.6	7
<i>Plantago lanceolata</i>	16.6	1.2	3.2	0.2	6	18.2	1.9	3.1	0.3	7	10.5	0.6	2.4	0.1	6	14.3	1.0	2.7	0.2	7
June						BM	SE	Si	SE	<i>n</i>						BM	SE	Si	SE	<i>n</i>
Meadow grasses						72	8	10.4	1.3	7						309	48	3.1	0.2	7
<i>Achillea millefolium</i>						139	21	13.0	1.9	7						7	2	4.0	0.5	6
<i>Daucus carota</i>						70	11	1.8	0.1	7						17	2	1.1	0.1	7
<i>Phalraia arundinacea</i>						23	5	12.9	2.0	7						45	7	3.8	0.3	7
<i>Plantago lanceolata</i>						888	70	0.6	0.1	7						150	29	0.4	0.1	7
June						N	SE	P	SE	<i>n</i>						N	SE	P	SE	<i>n</i>
Meadow grasses						31.0	0.8	5.7	0.2	7						19.7	0.7	4.5	0.2	7
<i>Achillea millefolium</i>						25.8	2.0	5.6	0.3	7						17.9	0.8	3.7	0.2	6
<i>Daucus carota</i>						23.3	1.8	4.3	0.2	7						13.7	0.7	2.9	0.4	7
<i>Phalraia arundinacea</i>						31.0	1.6	5.3	0.4	7						17.4	0.9	2.9	0.1	7
<i>Plantago lanceolata</i>						20.6	2.4	3.8	0.4	7						9.7	0.5	2.4	0.1	7

Biomass on dry weight basis (g m^{-2}) is averaged over all 10 replicates for every treatment but for chemical nutrient analysis we only used maximally 7 (randomly chosen) replicates. Silicon (Si), N and P are indicated as relative contents in the plant tissue (mg g^{-1} dry weight). All indicated errors are standard errors (SE, n = number of replicates). Unmown treatments were not sampled in June

Discussion

Although abundant experimental studies have focused on N and P uptake in riparian vegetation, a controlled experiment which studies Si uptake

(relative to N and P) in detail, under changing environmental conditions, is surprisingly lacking. Riparian meadows, of which our experimental units were small-scale versions, have a high potential to influence the Si input into rivers. Often dominated by

Fig. 2 Total nitrogen (N), phosphorus (P) and silicon (Si) uptake in the vegetation of the different treatments. The *top panels* are for the total biomass, the lower panels for the biomass without *P. lanceolata*. The *error bars* indicate the standard deviation (OM oxie, mown; ONM oxie, unmown; ANM anoxic, mown; ANNM anoxic, unmown)

Fig. 3 Nitrogen (N):phosphorus (P), P:silicon (Si), and N:Si weight ratios in the vegetation in the different treatments. The *left panel* is for the total biomass, the right panel for the

biomass without *P. lanceolata*. The *error bars* indicate the standard deviation (OM oxie, mown; ONM oxie, unmown; ANM anoxic, mown; ANNM anoxic, unmown)

Si-rich grasses or sedges, they are likely among the most active processors of Si of all terrestrial ecosystems (e.g. Blecker et al., 2006; Sommer et al., 2006; Struyf & Conley, 2009).

P concentrations in our experiment (the 4 dominant species contain on average 3.7 mg g^{-1} dry weight) were high compared to other studies, while N concentrations (18.7 mg g^{-1} dry weight) were high but not uncommon (Güsewell & Koerselman, 2002). Our experiment was, given the high supply of N and

P through fertilisers and the relatively high concentrations of N and P in plant tissues, clearly representative for a set of riparian meadows in an eutrophied environment, with N less available compared to P (but neither should be considered limiting at measured concentrations). In such eutrophied environments, wetland restoration and protection is often implemented as a measure to reduce N and P export. It is a well-established concept that controlling N and P export upstream by implementing riparian

vegetations is one of the most effective ways to control N and P fluxes through river basins, and in the end, to the coastal zone (e.g. Withers & Jarvis, 1998; Hattermann et al., 2006).

Waterlogging, mowing and relative Si uptake

In our experiment, two dominant species (*P. arundinacea* and *A. millefolium*, which contain over 1 wt% ASi) and the meadow grass cluster can be identified as Si accumulators. This is consistent with previous literature studies (Hodson et al., 2005). In general, monocots (e.g. *Poaceae*) contain more Si than dicots. The dicot-monocot division is only a general pattern, and deviations are not an exception. Although a dicot, *A. millefolium* was previously identified as a substantial accumulator of silicon (Hodson et al., 2005). Interestingly, nearly all the species in the waterlogged treatments had a lower ASi content compared to the non-waterlogged treatments. This contrasts with the Si content in soil solution, displaying higher concentrations in waterlogged anoxic ($115 \pm 32 \mu\text{mol l}^{-1}$) than in oxic conditions ($45 \pm 5 \mu\text{mol l}^{-1}$). Dissolved Si content in soil solution and plant Si content were thus not directly linked in our experiment, although such a link was found in other experiments (e.g. Henriot et al., 2006).

In the experiment, relative uptake of Si in vegetation halved because of mowing practices only. This was mainly because mowing favoured the abundance of the non-Si accumulating species *Plantago lanceolata*. Si uptake in Si accumulators on the other hand was apparently higher under oxic conditions. This has consequences which might be important to ecosystem engineers, trying to mediate nutrient fluxes. Riparian meadows, established to reduce nutrient fluxes to the coastal zone, might remove significantly less Si, especially relative to N and P, if mowing is applied in spring and if this enhances Si-excluder growth as it did in our experiment. This could be considered a positive effect from a management point of view. Indeed, decreased relative uptake of Si compared to N and P might positively affect N–P–Si ratios in rivers and estuaries during times with risk of DSI depletion.

On the other hand, uptake of Si into grass and/or sedges has been linked to an increased burial of ASi near the surface of floodplain wetlands (Struyf et al., 2009). This increased storage of ASi near the surface

can enrich wetland pore-waters with ASi (Struyf et al., 2005, 2009), which can in turn affect the exchange of DSI between wetlands and rivers. The storage of ASi in sediment and litter has been linked to an increased DSI export during low ambient DSI concentrations in tidal rivers (Struyf et al., 2006, 2007). Release of DSI from plant phytoliths has also been shown experimentally (e.g. Frayse et al., 2010). Reducing the DSI buffering capacity of riparian zones through the yearly removal of the standing crop could potentially lower this Si-buffering capacity of riparian zone to the adjacent rivers. This is an undesired effect in the context of eutrophication.

Perspectives

Our understanding of Si biogeochemistry in riparian meadows, also in those constructed specifically to control nutrient fluxes, is as of yet too limited to evaluate the trade-off between the removal of N and P (and thus also Si) on the one hand, and the creation of potentially Si buffering litter layers (possibly also releasing N and P) on the other hand. In order to implement the control of Si fluxes in the design and management of riparian meadows and small-scale wetlands aimed at reduction of the local output of pollutants and N (e.g. individual factories and households, not directly connected to a general sewer and treatment system), we will need significant progress in our understanding of the functioning of these systems in the Si cycle. Both in situ and ex situ experiments, aimed at testing the importance of specific processes (such as ours) and in situ budget studies, would be valuable in this context.

Interesting topics include:

- How quick is the recycling of biogenic Si in wetland and meadow soils, and how efficient is this process? Is this recycling complete, or is part of the biogenic Si buried permanently?
- How much dissolved Si is exchanged between riparian meadows and adjacent rivers, and how tight is the coupling between vegetation and soil biogenic Si?
- What is the in situ effect of the specific management of soil redox status, vegetation removal, drainage and hydrology?

- Is it possible to optimize the nutrient ratios released from riparian meadows designed for nutrient removal, by stimulating dissolved Si release to the river, while improving N and P removal?

In the latter context, it is interesting to note that in our experiment, the Si accumulators dominated the waterlogged treatments, resulting in a higher relative Si uptake in vegetation. This will increase the reactive biogenic Si content of the riparian meadow soil, potentially resulting in an increased buffering capacity of Si available in rivers. At the same time, waterlogged conditions might favour nitrogen removal through denitrification (Hill, 1996), but could also favour the release of dissolved orthophosphate into pore-water and thus potentially to the river (Loeb et al., 2008).

Conclusions

Understanding ecosystem resilience and buffer capacity, and how human interference has affected it, is essential to manage negative effects of human impact on these ecosystems (Gunderson, 2000). Land use and vegetation cover have undergone and still undergo huge changes through human intervention. For example, between 50 and 80% of wetlands have been lost from European and North-American estuaries (Elliott & Cutts, 2004), and have been replaced by urban or agricultural surfaces. In Midwestern States (USA), 80% of the wetland acreage has been drained (Mitsch et al., 2001). It has been well documented that this has reduced the resilience of aquatic systems to increased N and P concentrations, increasing the effect of excessive human N and P input. Wetland restoration programs are often based on this understanding.

In our experiments, only a small shift in vegetation coverage, induced by two changed (and manageable) environmental factors, had a relatively strong effect on the Si uptake by plants. This implies that ecosystem managers should take the potential influence of riparian meadows on Si fluxes into account, if these are restored to counteract eutrophication. However, to be able to do so, it is essential to quantify the trade-off between the two effects of Si uptake in riparian vegetation on the Si dynamics in the aquatic environment:

- Temporary reduction of Si fluxes to rivers through the uptake in silicon accumulating vegetation;
- The build-up of a biogenic silicon rich surface layer as a result of Si uptake into riparian vegetation, which potentially influences Si dynamics in the adjacent river.

Our concept of Si biogeochemistry in riparian meadows, also for those constructed specifically to control nutrient fluxes, is as of yet too limited to evaluate this trade-off.

Acknowledgments L. Clement and E. De Bruyn analyzed Si concentration in samples in the “UA, University of Antwerp, Department of Biology, Testing Laboratory for Chemical Water Quality”. Tom Vanderspiet analyzed N and P concentrations. Eric Struyf (post-doc) and Wout Opdekamp (aspirant) acknowledge personal financing by EU Marie-Curie Programme (FP6) and/or FWO (Research Foundation Flanders). Wiktor Kotowski acknowledges the Francqui Foundation for financing his research work at Antwerp University. We are also thankful to all students, who helped in the species harvesting and sorting.

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