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Consequences of different cutting regimes on regrowth and nutrient stoichiometry of *Sparganium erectum* L. and *Potamogeton natans* L. *River Research and Applications*. 33(9): 1420–1427

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Abstract

Aquatic vegetation forms an essential component in freshwater ecosystems but due to changed environmental and anthropogenic conditions often needs management to reduce nuisance for human land-use. In this paper the authors looked at the regrowth of two macrophyte species (*Potamogeton natans* and *Sparganium erectum*) in two lowland rivers under different cutting treatments. After an initial cross-sectional transect was manually removed from bank to bank at the beginning of the growth season, a monthly repetitive removal of biomass in plots on that transect was done during the rest of the growth season (testing frequency of mowing). Additional new transects were also cut in subsequent months (testing timing of mowing). Finally, biomass was repetitively removed in plots in those additional transects too (testing frequency \times timing of mowing). The biomass at the end of the growth season was analysed for C, N, P and Si. It was demonstrated that timing and frequency of vegetation cutting has an important effect on the capacity and rate of species' recovery, and therefore on the efficiency of the applied management. Nutrient stoichiometry of the regrown biomass was directly affected by cutting. Caused by differences in the applied timing and frequency of the cutting, C/N and N/P ratios and BSi concentrations were highly variable. Yet overall there was a clear tendency towards a higher C/N ratio and BSi concentration, and lower N/P ratio in biomass that recovered after cutting. This human impact on the quantity and quality of autochthonous organic matter may have knock-on effects on the decomposers food web and mineralisation process.

Keywords: aquatic vegetation, carbon, phosphorus, silicon, nitrogen, Nete Catchment

Introduction

Aquatic vegetation is an essential biotic component in natural stream ecosystems. Excessive growth of aquatic plant biomass in eutrophic water bodies has been reported especially in temperate rivers of western and central Europe (Quilliam *et al.*, 2015 and reference therein). The presence of macrophytes increases the hydraulic resistance of the channel, leading to a reduced drainage capacity and increased water levels (Bal *et al.*, 2011; Bal and Meire, 2009). River margins and the neighbouring lands are often used for human purposes such as housing and agriculture and managing water levels is therefore of crucial importance. Upstream water retention in (restored) wetlands is a sustainable measure reducing downstream water levels. Yet ad hoc mitigating measures are often needed to locally reduce flooding or water logging risks. This is usually done by mechanically removing the majority of the vegetation, either by extracting whole plants e.g. rototilling or hydro-racking, or by cutting the vegetation just above the sediment e.g. mechanical cutting and collection. The former techniques remove all plant parts resulting in the bycatch of aquatic animals, increased turbidity and decreased oxygen levels. In addition plant fragments are created from which new plants can develop downstream (Quilliam *et al.*, 2015). In contrast, the latter technique reduces the impact on the sediment and on the bycatch of aquatic fauna, and is therefore preferred from an ecological point of view. Yet it allows for rapid regrowth to occur from the root systems (Perkins and Sytsma, 1987; Strange *et al.*, 1975; Quilliam *et al.*, 2015). Within three to six weeks after cutting, similar plant biomass can be attained (Rawls, 1975; Cooke *et al.*, 1990; Crowell *et al.*, 1994; Bal *et al.*, 2006) requiring an additional second or even a third cutting to ensure sufficient drainage. Kimbel and Carpenter (1981) have shown that *Myriophyllum aquaticum* biomass is reduced when cutting is done from July onwards, thus the timing of removal may determine the regrowth potential of the vegetation and the frequency of the maintenance needed. In general, regrowth is slower when cutting is done at the time belowground reserves

of the vegetation are lowest, which for most aquatic plants is just before the peak of the aboveground biomass (Linde *et al.*, 1976). This peak in aboveground biomass depends on both species composition and management history. Indeed, cutting can change species composition in rivers because the regrowth capacity is species dependent. *Potamogeton pectinatus* for instance, a fast growing species tolerant to trimming has physiological adaptations allowing it to rapidly elongate its stem under anoxic conditions (Dixon *et al.*, 2006). This gives it a head start when grown from a tuber. The cutting frequency will also influence the species composition by favouring fast growing species (Haslam, 1978; Grime, 1979). For example in Danish lowland rivers *Sparganium emersum*, mowed once or twice a year with its basal meristem left intact, was recorded to out-compete faster growing species (Sand-Jensen *et al.*, 1989; Baattrup-Pedersen *et al.*, 2002). This was however, not confirmed by other studies which found no effect of weed cutting on the coverage of *S. emersum* in German rivers (Wiegand *et al.*, 2014).

Cutting also has an effect on nutrient cycling in rivers whereby the removal of aquatic foliage results in a decrease of hydraulic resistance and water retention, which negatively influences biogeochemical processes such as denitrification (Seitzinger *et al.*, 2006). Insufficient hydraulic resistance results in higher current velocities, which may lead to decreased sedimentation and the accretion of organic matter and particulate nutrients. Studies report accumulation of organic matter in macrophyte patches up to 3 to 4 (Kleeberg *et al.*, 2010), 6 (Schoelynck *et al.*, 2014) and >10 times (Sand-Jensen, 1998; Cotton *et al.*, 2006; Schoelynck *et al.*, in press) greater than in non-vegetated sediments. By the removal of macrophytes, the biomass fixed nutrients are also removed and the biomass can be used as fertilisers on agricultural land (Quilliam *et al.*, 2015). However, this is not commonly done in Western Europe because high costs are involved in the transport and processing of the biomass, as well as the availability of relatively cheap industrial fertilisers and current legislation

(Boerema *et al.*, 2014; Quilliam *et al.*, 2015). Biomass is therefore usually thrown along the river banks from which nutrients rapidly leach back into the river (Boerema *et al.*, 2014).

Less studied, is the effect cutting has on the nutrient stoichiometry and content in the vegetation. For example the concentration of P in the leaves of emergent species such as *Phragmites australis* is limited because they store most of it in their rhizome system (Wersal *et al.*, 2013), whereas many rooted submerged aquatic plants translocate P from their above-ground parts to the rhizome only in the latter part of the growing season, before senescence (Quilliam *et al.*, 2015). Changing the composition of the vegetation may thus change the timing and the amount of nutrients in the different plant parts. An even more direct effect, that of cutting regimes on plant nutrient stoichiometry (rather than on changing the vegetation) is to our knowledge unknown and hence forms part of the focus of this study. Yet parallels can be drawn with terrestrial vegetation where cutting or herbivory causes plants to experience several growth cohorts per year resulting in the change in nutrient content (Bardgett *et al.*, 1998). In the Biebrza mires (Poland) for example, annual hay-removal affected the P concentrations in vascular plants, and therefore N:P stoichiometry was severely altered (Venterik *et al.*, 2009). Opdekamp *et al.* (2012) showed in the same Biebrza mires that Si in grasses and sedges was significantly lower when frequently mowed, most likely due to an age effect of the tussock forming shoots in the unmown situation. In contrast, Massay *et al.* (2008) and McNaughton *et al.* (1985) showed that Si concentration in grasses is positively correlated to grazing pressure by voles. For macrophytes, an increased Si uptake is recognised as a reaction to plant stress in general (including hydrodynamic stress, nutrient stress and herbivory; Schoelynck and Struyf 2016).

Changes in nutrient stoichiometry of wetland plants cannot be underestimated as it is one of the major factors controlling the decomposition rate of plant litter and the decomposers' food web. See for instance the experiments by Emsens *et al.* (2016a) on sedges grown under

eutrofied (NPK) conditions, or experiments by Schaller and Struyf (2013) for *Phragmites australis* grown under increased Si conditions: all demonstrated that an altered nutrient stoichiometry has an effect on bacterial and/or macro-invertebrate breakdown processes, and this could be also true for litter from riverine plants. Timing and frequency of cutting could strongly affect quantity (amount of biomass) and quality (nutrient ratios) of macrophyte organic matter and therefore its decomposition, which plays a major role in nutrient cycling (Webster and Benfield, 1986) and carbon sequestration (Gessner *et al.*, 2010; Regnier *et al.*, 2013) in rivers and wetlands, but remains poorly understood. The objective of this study was to evaluate the effect of different timing and cutting frequencies on the regrowth capacity and nutrient stoichiometry of the emergent species *Sparganium erectum* L. and rooted floating-leaved species *Potamogeton natans* L. This was tested *in natura* with different cutting regimes.

Material and Methods

Study location and set-up

The experiments started in May 2010 and lasted for 5 months in two lowland rivers in the Nete catchment, Belgium. These sites were selected because the vegetation was dominated by *Potamogeton natans* and *Sparganium erectum* respectively for the Desselse Nete and Sloopbeek. These two streams flow through a nutrient rich agricultural environment and have a eutrophic status (Table 1).

In both streams an initial cross-sectional transect (t1) of 1.5 meter long was manually removed from bank to bank in May to determine the initial biomass. Removal was carefully done by cutting the stems just above the sediment to reduce disturbance of the sediment and the collected plant material was weighed. One month after the first cutting, a quarter of the initial transect was recut (p1.4) to determine the regrowth after one month. The procedure followed is illustrated in Fig.1 whereby the first digit refers to the month of initial cutting, and the second digit refers to the frequency the plot was mowed (including the initial cutting). A second transect (t2) of 1.5 m long was also cut in the same way and sufficiently downstream of t1 to avoid interference. In July plot p1.4 was recut together with a new plot (p1.3) on transect t1. On transect t2 a first plot p2.3 was cut and a new transect t3 was cut similar to the previous transects. This procedure was repeated every month according the schedule in Fig.1. Finally, in September, all plots and an undisturbed reference transect t5 was mowed to determine biomass and nutrient content.

Chemical analysis

Only plots sampled in September (n=10) and an extra reference transect (t5) in that month were analysed because it is this biomass that will naturally die-back and become litter. The plant material collected per plot was dried at 70°C until a constant mass was reached (2 days

in general). After weighing dry mass, grinding and homogenising the samples, total N and total P content were determined according to Walinga et al. (1989). Samples were digested with H₂SO₄, salicylic acid, H₂O₂ and subsequently analysed on a colorimetric segmented flow analyser (SAN⁺⁺, Skalar, Breda, The Netherlands). The organic matter content was determined by loss on ignition (Heiri *et al.*, 2001). Samples were heated to 105 °C for 2 h and weighed. Thereafter, samples were ignited at 550 °C for 4 h and weighed again. The difference in mass gives an index of the organic matter present in the sample. Dividing organic matter by 1.8 gives the amount of carbon present (in mg/g) (Schlesinger, 1977; DIN38414/S3, 1985). Biogenic silica (BSi) was extracted from 25 mg of dry plant material by incubation in a 0.1 M Na₂CO₃ mixture at 80 °C during 5 h (DeMaster, 1981). The extracted and dissolved silica was analysed on a colorimetric segmented flow analyser (SAN⁺⁺, Skalar, Breda, The Netherlands). The extraction process in 0.1 M Na₂CO₃ at 80° has been well established and tested since it is capable of fully dissolving the BSi from plant phytoliths at the solid-solution ratios and extraction time we applied (Saccone *et al.*, 2007).

Statistics

The coefficient of variance (cv) is defined as the ratio of the standard deviation to the mean and was calculated for C/N ratio, N/P ratio and BSi concentration in September of the 10 examined cutting treatments. A Shapiro-Wilk normality test indicated normal distribution of these datasets. A Students-t test was used to test whether values of the reference transect t5 were significantly different from the treatment values (95% confidence interval). All calculations were performed in R(v.3.2.0.).

Results

The biomass peak for *S. erectum* was reached in June 2010 with a total dry biomass (DM) of 0.9 kg m⁻². For *P. natans* a maximum DM of 0.3 kg m⁻² was reached in August 2010 (Fig 2a and b). When cut for the first time in May, *S. erectum* recovered in biomass after one month of regrowth comparable with the uncut situation in that month. When cut for the first time in June *S. erectum* only recovered, i.e. reached similar biomass as the uncut situation, after three months in September (blue vs green bars in Fig. 1). When the vegetation was cut after June a great reduction in biomass (DM) was seen later in the vegetation season (blue vs purple or orange bars Fig. 2). For *P. natans* the outcome was similar but regrowth was slower and later in the season. When cut in May vegetation only reached preharvest values after two months but never reached preharvest values when first cut later in the season (35% lower). When first cut from June onwards, biomass production was lower for both species.

Increasing cutting frequency resulted in a higher reduction of biomass later in the growing season compared to the uncut treatment. To evaluate the frequency of recutting, biomass days (g day m⁻²) were calculated for different cutting treatments (i.e. combination of timing and frequency, represented by the different plots and plot labels in Fig. 1), which is the integration of the biomass over the period of time this biomass was present. It is calculated by using the sum of the biomass production per month, multiplied by the amount of days between each sampling period (roughly equalling one month period). For both species, the treatment resulting in the highest accumulated biomass is the uncut situation. If only one cutting effort a year is desired, the best month is May (treatment represented by plot 1.1) and June (represented by plot 2.1) for *S. erectum* and *P. natans* respectively. If cutting twice a year is a precondition, the treatment represented by plot 1.2 for *S. erectum* and by plot 2.2 for *P. natans* results in the lowest accumulated biomass, i.e. cutting in May-August and June-August respectively. More frequent cuttings generally result in an even lower accumulated

biomass, and the treatment resulting in the lowest biomass days along the entire vegetation season is to cut every month (Table 2).

C/N ratio of the mowed *P. natans* plots shows very little variation (coefficient of variance, $cv = 0.06$) with a 50 percentile (d50) around 15.6 (Fig. 3). The September transect (C/N = 15.8) equals the d50 indicating there is no significant effect of cutting on the C/N ratio of *P. natans* biomass in September ($p=0.69$). C/N ratio of the mowed *S. erectum* plots shows variation ($cv = 0.29$; $d50 = 21.2$), and the September transect (C/N = 26.5) lies between d25 and d50. Although not significantly different ($p=0.13$), this indicates that different cutting treatments result in *S. erectum* biomass with a different and mostly higher C/N ratio, depending on the treatment. Cutting in May, July and August (treatment represented by plot p1.3) for example, has a maximum C/N ratio of 31.2, which is twice the value of the reference transect.

N/P ratio of the mowed *P. natans* plots also showed very little variation ($cv = 0.07$; $d50 = 7.4$). The September transect ratio (N/P = 6.8) is significantly ($p<0.01$) lower than the d25 quartile, but given the small amount of variation, there is likely only a minor effect of cutting on the N/P ratio of *P. natans* biomass in September (Fig. 3). The N/P ratio of the mowed *S. erectum* plots shows a lot of variation ($cv = 0.22$; $d50 = 6.5$), and the September transect ratio (N/P = 8.3) is significantly higher ($p<0.05$) and lies above d75. This indicates that different cutting treatments result in *S. erectum* biomass with a different and mostly lower N/P ratio, depending on the treatment. Cutting in June and August (treatment represented by plot p2.2) for example, has a minimum N/P ratio of 4.7, which is nearly half that of the reference control transect.

The BSi concentration in the mowed plots of both species shows variation ($cv = 0.19$; $d50 = 1.6 \text{ mg g}^{-1}$ for *P. natans* and $cv = 0.51$; $d50 = 0.6 \text{ mg g}^{-1}$ for *S. erectum*). For both species, the BSi concentration of the reference transect (0.7 and 0.1 mg g^{-1} respectively) is significantly

lower than the absolute minimum measured in the mowed plots ($p < 0.001$ for both species; Fig. 3). This means that cutting results in a strong increase in BSi concentration for both species: up to 2 times for *P. natans* when cutting in July (treatment represented by plot p3.1), and up to 13 times when cutting in May and August (treatment represented by plot p1.2).

Discussion

The initial growth rate of the natural vegetation in our study is fast and reaches a maximum biomass in summer (June for *S. erectum* and August for *P. natans*), comparable to that of other studies in streams, e.g. up to 0.11 kg DM m⁻² (Chambers *et al.*, 1991) and up to 0.29 kg DM m⁻² (Bal *et al.*, 2006). After August, vegetation generally starts to die-off and biomass rapidly decreases (Sand-Jensen *et al.*, 1989; Bal *et al.*, 2006). Note that due to the changing climatic conditions from year to year and depending on hibernation type some ‘wintergreen’ may be present throughout the winter season (Wiegleb *et al.*, 2014).

The regrowth of the studied species is rapid after a single early-season cutting in May and biomass reaching an equivalent biomass to that in the control after a period of 3 to 6 weeks. Other studies report a similar recovery period (e.g. *Myriophyllum aquaticum* and *Potamogeton pectinatus* (Rawls, 1975; Cooke *et al.*, 1990; Bal *et al.*, 2006)). Hence cutting early in the growing season has no sustainable effect for the rest of the summer.

Repetitive cutting always results in reduced recovery and a permanent low(er) biomass during the whole season. When translated towards species diversity this might imply a decline instead of a theoretical hump-backed shape response according the intermediate disturbance hypothesis (Connell, 1978; Wilkinson 1999). However the studied plots were dominated by one species and upscaling of our results towards implications on diversity is very difficult and out of the scope of our results. We used the accumulated biomass over the growing season (biomass days) to compare the different cutting treatments. Because cutting is expensive and has ecological drawbacks (Boerema *et al.*, 2014), we selected the various treatments ad hoc with a maximum of 2 cuttings a year. This is a realistic approach and is being put in practice in this catchment. Consequently, the May-August treatment came out best for *S. erectum*, and the June-August treatment for *P. natans*. These findings can be used

as guidelines in future management strategies, though a case-specific approach is often needed for which we provide two arguments:

First, the shift of 1 month between the optimal strategies of both species is to a great extent attributed to the fact that *S. erectum* starts growing 1 month earlier and reaches maximum biomass sooner than *P. natans*. This is a species property, but likely also influenced by the location where it grows (river depth, light conditions, prevailing current velocities...) which may be very different from the reaches tested in this study. A good approach to determine the start of the growing season might be the 'accumulated temperature method' proposed by Soetaert et al. (2004). By monitoring the water temperature, the starting point of the growing season can be predicted. From that point onwards, a numerical aquatic plant growth model (e.g. logistic growth; Sukhodolova 2008) can predict the moment of maximum biomass. The management strategy could be adjusted to this model.

Second, the selected optimal cutting strategy does not account for sudden events. Notwithstanding the demonstrated unsustainability of early-season cutting (because of rapid regrowth), cutting during this period is sometimes needed to anticipate harsh weather conditions, or to prevent water logging of agricultural or urban areas. Risk analyses were not included in this paper, but obviously should be taken into account on a case by case treatment. Boerema et al. (2014) make, for instance an economic evaluation of vegetation removal on catchment scale. It turns out that the benefits (or losses) vary greatly in a wet summer year vs. a dry summer year.

It is also expected that the time at which a disturbance takes place, could strongly influence the regeneration of certain species. *Potamogeton pusillus*, for example, will not regenerate from detached fragments when mowed early in the growth season, but does so when mowed later in the season (Barrat-Segretain *et al.*, 1996; Kadono, 1984). Additionally, frequent weed

cutting would favour the growth of species like *Sagittaria sagittifolia* and *Sparganium emersum* because shoots can originate from their basal meristem typically situated 6 cm deep in the sediment (Sand-Jensen *et al.*, 1989). This gives these species a competitive advantage in this situation, as they can start growing immediately and don't have to invest in the formation of a new meristem. Alternatively, when many plant fragments are left in the stream after cutting, species with multi-apical meristems such as many invasive species have advantages, e.g.: *Myriophyllum spicatum* and *Egeria densa* in Canada and USA, or *Ceratophyllum demersum* in China (Vari, 2013 and references therein). The advantage for plants having multiple meristems is that they need not invest energy and resources to generate new shoots after having been cut. Both strategies (basal vs apical meristem) enable species to recover relatively fast after cutting, depending on the method used (mechanical cutting with collection vs. rototilling or hydro-racking). Mainly species with a single apical meristem suffer from weed cutting and can disappear completely (Cavalli *et al.*, 2014). The studied species *P. natans* and *S. erectum* have a multi-apical and basal meristem respectively (Cavalli *et al.*, 2014). In our set-up the plants also most likely recolonised from underground parts as the dense vegetation upstream of the cut plots would filter out most fragments from which recolonization would occur. This is also seen in the hypothesised border effect by Barrat-Segretain *et al.* (1998). The same authors have shown that *Sparganium emersum* is able to recolonise quickly by producing roots. In contrast *Potamogeton pusillus* was unable to regenerate.

Macrophytes can reach a high standing biomass fulfilling an important role in the nutrient cycling of streams (Webster and Benfield, 1986; Battle and Mihuc, 2000). Plants can take up nutrients from the water and store it temporarily until plants die-off in autumn. This nutrient storage is obviously determined by available nutrients and specific growth characteristics of

the species, but this study shows that it can also be caused by human disturbance (*in casu*: cutting). Nutrient ratios C/N and N/P were not influenced in *P. natans* (a significant but slightly lower N/P at best), but they were significantly influenced in *S. erectum*. Depending on the applied timing and frequency, both ratios were very variable, with peaks at almost double (C/N) or half (N/P) the September reference values. Overall, there was a clear tendency towards a higher C/N ratio, and lower N/P ratio in the mowed plots compared to the September reference transect. At the same time, BSi increased significantly by a factor 2 or more in both species when they experienced cutting. Increased BSi in macrophytes under stress caused by hydrodynamic disturbance was shown earlier (Schoelynck *et al.*, 2012, 2015). Almost certainly, the plants experience cutting as a severe stressful disturbance to which they likely responds with increased Si uptake. It is said that Si may change macrophyte nutrient ratios in general (Schaller *et al.*, 2012; Schaller *et al.*, 2015), which may explain the shifts in C/N and N/P ratios we've observed. Litter stoichiometry is one of the factors controlling microbial decomposition: low N/P ratios and high C/N ratios are good predictors of poor organic matter quality and of low decomposition rates (Aerts and De Caluwe 1997, Gusewell and Gessner, 2009). Emsens *et al.* (2016b) demonstrated that anthropogenic nutrient enrichment of wetlands leads to consistently lower (up to 50 % reduction) litter Si concentrations in all tested *Carex* species, suggesting a plant-physiological response following the relief of nutrient stress. A negative correlation between litter Si concentrations and litter decomposition rates under nutrient poor conditions suggested an inhibiting effect of Si on decomposition. However, positive correlations between litter Si concentrations and C:N and lignin:N ratios indicated a strong interdependence of Si with other litter quality parameters that determine decomposition. An elaborated decomposition study was done by Schaller and Struyf (2013) on reed, whereby litter from plants exposed to high Si availability degraded up to 90 % faster than controls. In the presence of macro-invertebrate shredders

however, degradation rates actually decreased when litter was more Si rich. This points to a negative effect of Si in litter on shredder functionality, and thus on total decomposition rates. It is clear that more and specific research is needed to determine whether these observed changes in stoichiometry (N/P, C/N, Si) have any significant effect on the litter breakdown in lowland rivers.

We conclude that timing and frequency of cutting macrophytes has an important effect on the regrowth of the species and therefore on the efficiency of the applied management treatment. Moreover this study is one of the first to demonstrate that cutting can also directly influence nutrient stoichiometry of the biomass which is important in decomposition. This human impact on the quantity and quality of autochthonous organic matter may have knock-on effects on the decomposers food web and mineralisation process.

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Table 1: Basic stream characteristics of the investigated stretches. Data are averages over the period May-September 2004 (Slootbeek) and May-September 2010 (Desselse Nete). More elaborate overview of the discharges can be found in Bal and Meire, 2009.

	Desselse Nete	Slootbeek
Average width (m)	4.0	2.0
Discharge ($\text{m}^3 \text{s}^{-1}$)	0.35	< 0.1
NO_3^- (mg L^{-1})	0.73	0.29
NH_4^+ (mg L^{-1})	0.18	0.35
PO_4^{3-} (mg L^{-1})	0.04	0.07
DSi (mg L^{-1})	7.3	21.7
pH	6.9	6.7
Electric conductivity (μScm^{-1})	387	236

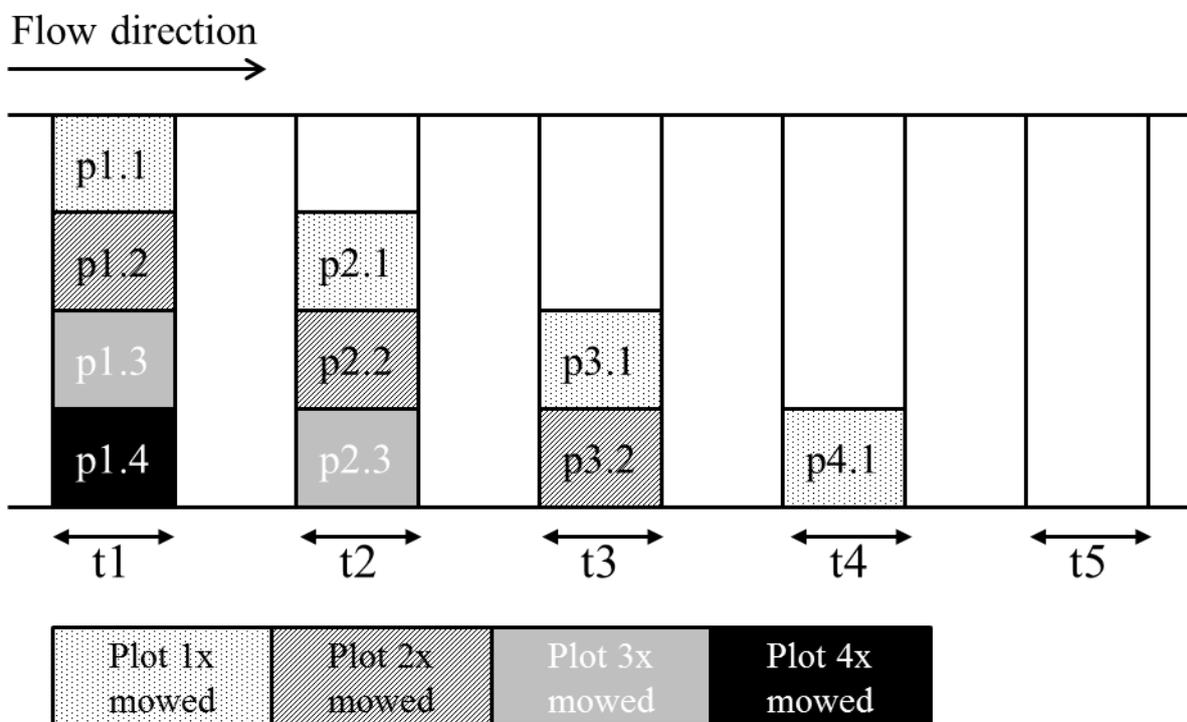
- 1 **Table 2:** Overview of Biomass days resulting from different cutting regimes during the
 2 growth season (May-August). The symbol × marks the months in which biomass was
 3 removed.

Transect/ Plot Nr	Times mowed	Months in which was mown				Biomass days (kg.day.m ⁻²)	
		May	June	July	August	<i>Sparganium erectum</i>	<i>Potamogeton natans</i>
p1.1	1	×				46	23
p1.2	2	×			×	36	18
p1.3	3	×		×	×	30	13
p1.4	4	×	×	×	×	15	8
p2.1	1		×			59	13
p2.2	2		×		×	48	11
p2.3	3		×	×	×	38	8
p3.1	1			×		57	16
p3.2	2			×	×	57	14
p4.1	1				×	75	23
Reference t5	0					87	30

4

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6 **Figure 1:** Schematic overview of the plots in both rivers. Each month, from May to August,
 7 all biomass was cut for the first time on a transect (t1 to t4). In months subsequent to the first
 8 removal, plots on these transects were recut. The number of the plots is schematic with the
 9 first digit referring to the month of initial cutting, and the second digit referring to the
 10 frequency the plot was cleared (including the initial mowing). The cutting frequency is also
 11 visualised by the grey scale. An undisturbed reference transect (t5) was additionally cut in
 12 September at the end of the growing season.

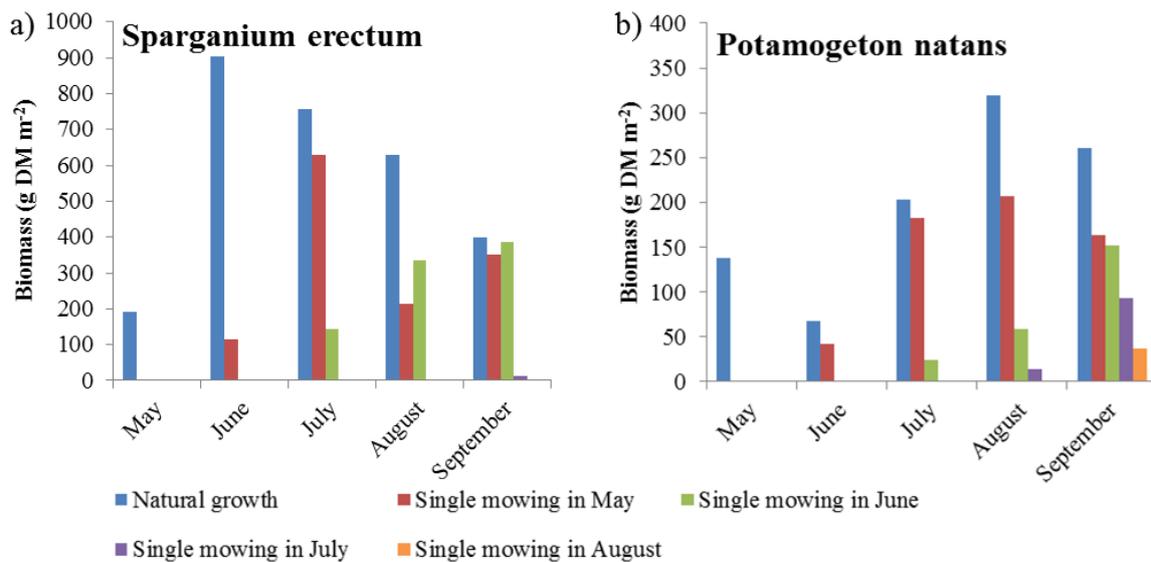


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15 **Figure 2:** Monthly dry biomass of *Sparganium erectum* (a) and *Potamogeton natans* (b)
 16 when not removed (natural growth; blue bars) and when a single cutting regime was executed
 17 in different months. For example, when biomass was removed in June, then the biomass is
 18 displayed by the first 2 blue bars and from July onwards by the 3 successive green bars. Data
 19 from multiple cutting regimes are not shown here (see table 1).

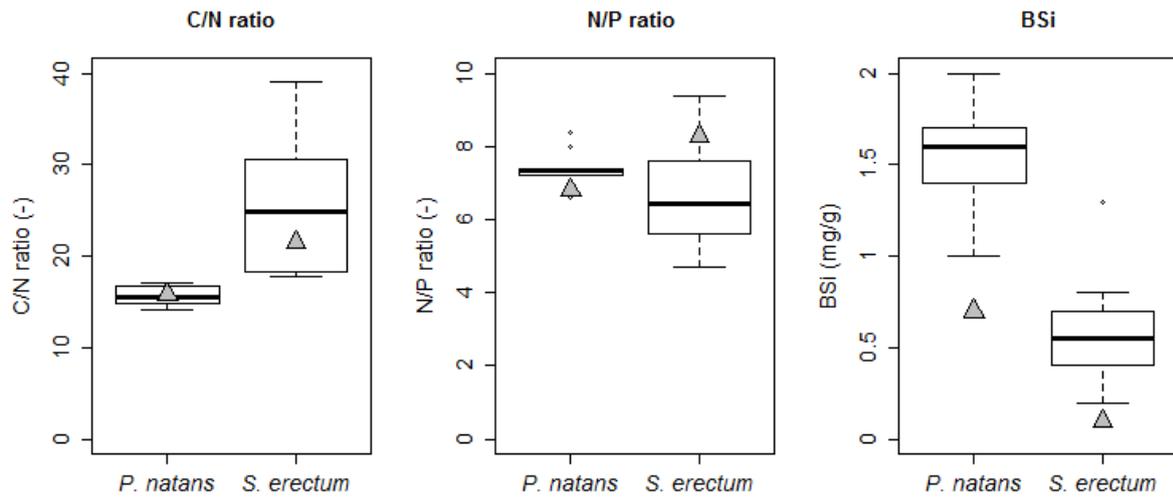
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23 **Figure 3:** These boxplots show the 25, 50 and 75 percentiles of the variation of C/N ratio,
24 N/P ratio and BSi concentration in September of the 10 examined cutting regimes. The
25 overlaying grey triangle is the corresponding ratio or concentration of the reference transect
26 (t5) in September.



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