

ABSTRACT

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Submerged macrophytes in Big Spring Creek, WI: Distribution and influence on phosphorus dynamics

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Abstract:

Submerged macrophytes affect many aspects of lotic ecosystems, including nutrient dynamics. We performed longitudinal vegetation surveys to describe the distribution of macrophytes in Big Spring Creek, Wisconsin. We also measured environmental factors and used *in situ* mesocosms to estimate Soluble Reactive Phosphorus (SRP) uptake by submerged macrophytes. Biomass ranged from 1.5 g/m² to 60.3 g/m² throughout the year. Below-canopy Photosynthetically Available Radiation (PAR) and water velocity were the most significant indicators of plant biomass in the stream. Macrophytes had an uptake rate in the range of 364.3-573.5 μg/m²/day, resulting in a maximum uptake potential of 0.0029 -0.0045% of daily SRP load. Although macrophytes in Big Spring have normal SRP uptake capabilities, this results in very little impact on the nutrient dynamics in the system.

Introduction:

The submerged macrophyte community is an important component of many lotic ecosystems, as it performs many critical ecosystem functions. In many riverine systems, where flow velocity washes algae downstream, submerged macrophytes are dominant primary producers and can serve as the base of the food chain when they die and become food for detritivores (Sprenkle *et al.*, 2004). In addition to driving the riverine food chain, macrophytes provide habitat for macroinvertebrates and small fish (Warfe and Barmuta, 2006). Macrophytes also act as dams, causing a backup in water and a decrease water velocity, which results in the settlement of suspended sediments (Madsen *et al.*, 2001; Horvath, 2002; Champion and Tanner, 2000). The presence of macrophytes can also affect the chemistry of riverine systems.

When particulate matter settles out of suspension, it may carry phosphate and ammonium ions with it, thus altering the concentrations of these nutrients in the water column (Wilcock *et al.*, 2002). Benthic sediments can also bind nutrients, effectively removing them from the water column, or they can release previously bound nutrients, thus adding nutrients to the water column (Wilcock *et al.*, 2002; Madsen *et al.*, 2001; Wade *et al.*, 2002). The interactions between sediments and nutrients, especially phosphorus (P), are often governed by the availability of oxygen, with P bound in the presence of oxygen and released in the absence of oxygen (Wilcock *et al.*, 2002).

Macrophytes and epiphytes also influence the retention and release of nutrients. Recent studies suggest that macrophytes are responsible for uptake and potential long-term retention of added P in streams (Meals *et al.*, 1999; Bernot *et al.*, 2006; Pelton *et al.*, 1998; Wade *et al.*, 2002). These studies imply that macrophytes could moderate the effects of large inputs of nutrients, especially P, in lotic systems. This effect is important, because many streams receive

large inputs of nutrients from surrounding agricultural fields in snow melt and storm events (Bernot, *et al.* 2006). These nutrients can lead to the eutrophication of larger rivers and lakes downstream, interfering with recreational or commercial use of these waterways (Bernot *et al.*, 2006; Champion and Tanner, 2000).

Because of the impact nutrients can have on aquatic ecosystems, it is important to understand how macrophytes interact with nutrients. In order to achieve this goal, we must understand what factors influence the distribution and abundance of macrophytes in aquatic systems. There have been many studies describing potential parameters governing macrophyte distribution. These parameters include light availability, temperature, water velocity, and substrate type (Lacoul and Freedman, 2006; Madsen *et al.*, 2001; Sprenkle *et al.*, 2004). Most plants have a minimum light requirement, which varies among species, and some may have a maximum light tolerance, above which they experience photoinhibition. Analogous limits also apply to temperature (Lacoul and Freedman, 2006; Sprenkle *et al.*, 2004). Concerning water velocity, many aquatic plants are more productive in moderate flow streams. The flow of water over the leaves decreases the size of the boundary layer, thus increasing diffusion rates of gasses and nutrients into the leaf. Lacoul and Freedman (2006) state that velocities of 0.3-0.4 m/s are ideal, while Madsen *et al.* (2001) suggest that velocities <0.1 m/s are ideal for submerged macrophytes. High velocity can inhibit some plants by damaging plant tissue or tearing the plant from its roots (Madsen *et al.*, 2001).

In some systems, especially oligotrophic streams, nutrient availability is the major limitation to macrophyte abundance. Nitrogen (N) and P are critical nutrients for plants and are most often the limiting nutrients in aquatic systems. Although nutrient concentrations can affect macrophyte growth and distribution, macrophytes also have the potential to affect nutrient

concentrations. Rooted submerged macrophytes have the ability to take up nutrients from both the sediments and the water column (Pelton *et al.*, 1998; Madsen and Cedergreen, 2002). Madsen and Cedergreen (2002) found that macrophytes are able to meet their nutrient needs solely through leaf uptake. Pelton *et al.* (1998) found that macrophytes take up P directly from the water, and the rate of this uptake increases with water P concentrations. Given that macrophytes have been shown to have the ability to take up nutrients from the water column, it is likely that they have a large role in determining stream nutrient concentrations.

The purpose of this study was two-fold. We first wanted to assess the general distribution of macrophytes in a south-central Wisconsin river. We then wanted to determine the potential role that macrophytes have in P dynamics in the river. We performed surveys of the vegetation in the stream, and we related plant distribution to light, temperature, water velocity, and nutrient data to understand what factors affect macrophyte distribution in the system. We also performed *in situ* mesocosm phosphorus-addition experiments to determine the Soluble Reactive Phosphorus (SRP) uptake potential of the macrophytes in the river.

Study Site:

We conducted this study in Big Spring Creek, a river in the town of New Haven, Adams Co., WI. Big Spring is a second-order river (Figure 1). The stream is predominately spring-fed, which results in relatively constant discharge. There is one dam in the center of our study reaches, and a second below our study reaches forms Lake Mason. The Big Spring watershed is 21.1 km². Agricultural fields (46%), forest cover (31%), grassland (21%) and wetland (2%) dominate the watershed of Big Spring, resulting in high nitrate and moderate phosphorus

concentrations. Ammonium concentrations are relatively low. Riparian vegetation ranges from reed canary grass (*Phalaris arundinacea*) to woody forest cover (Julian *et al.*, in prep). Although the base substrate of Big Spring is coarse clay material, many reaches of the river have fine silt substrates and are dominated by submerged macrophyte beds. The most common macrophyte species present in the river are *Potamogeton crispus*, *Zosterlla dubia*, *Elodea canadensis*, and *Nitella spp.* Another *Potamogeton* species, either *P. pusillus* or *P. foliosus*, is common. The two species are not distinguishable in the field and are referred to in this paper as *P. pusillus/foliosus*.

Methods:

Biomass Surveys:

In order to determine the abundance of submerged macrophytes in Big Spring Creek, we conducted vegetation surveys once a month from June-November in 2005 and from April-December in 2006. Winter months were not surveyed because macrophyte growth ceased and cover receded to nearly zero. Surveying resumed in the spring when vegetation returned. Transects were pre-determined by an accompanying study. A total of six reaches along the river were surveyed, two above the reservoir and four below the reservoir. The sites were labeled Up 1, Up 2, Dn 0, Dn 1, Dn 2, and Dn 3. Up 1, Up 2, and Dn 0 each had 2 transects, while Dn 1, Dn 2, and Dn 3 each had three transects (Figure 1). Transects within each reach were roughly 10 m apart. We measured channel width and estimated percent cover four times across the channel (every 20% of the width) using a 0.25 m² quadrat. Percent cover was estimated for each species present (*P. crispus*, *Z. dubia*, *P. pusillus/foliosus*, *E. canadensis*, and *Nitella*). Plants were

identified to the lowest taxonomical level possible in the field. We measured water velocity at the center of each quadrat at 60% of the water depth using a Marsh-McBirney current meter.

To convert our percent cover data to biomass data, we collected samples of each plant species outside the study reaches in the summer of 2005. At least 8 samples of each species were collected, with corresponding percent cover values ranging from 5% to 100%. We rinsed the samples to remove sediment, associated epiphytes, and macroinvertebrates and then dried the samples for at least 48 h at 60°C. After obtaining the dry-weight biomass (g/m^2), we performed a linear regression to find the relationship between percent cover and biomass for each species (Table 1). This procedure was necessary because we could not directly sample the study reaches due to the nature of our sampling regime. Average total macrophyte biomass and percent cover was obtained for each transect and site by survey date. Values excluded visible epiphyte growing on or around the macrophytes.

Distributional Study:

We collected data on several parameters in order to determine the factors that influence the distribution of submerged macrophytes in Big Spring. We sampled nutrients and measured temperature at Up 1, just above Dn 0, and at Dn 2. Daily averages of Photosynthetically Available Radiation (PAR) at the water's surface for May 15, 2006 to September 15, 2006 were determined for the whole stream using Gap Light Analyzer software (version 2.0; Frazer *et al.*, 1999) with canopy photos taken with a Nikon Coolpix 4500 to derive below-canopy irradiance (Julian *et al.*, in prep).

Nutrient samples were collected in 60 ml acid-washed LDPE plastic bottles. We filtered the samples in the field, rinsing the sample syringe and sample bottles three times with river

water. We kept samples on ice in the field. In the lab, samples were analyzed for SRP within 48 h of collection using the ascorbic acid molybdate photometric reaction and a spectrophotometer (Eaton *et al.*, 1995). Temperature data was collected as point data using temperature probes.

Using SigmaPlot software (version 9.0, Systat Software Inc.), we ran linear regressions between average biomass and the parameters measured in the distributional studies, including velocity from the biomass surveys. Monthly averages of nutrients and temperature were used in the analysis. Since the PAR data were averages from May to September, biomass data from the July survey were used in that regression. Log-transformed regressions were performed as necessary to obtain constant variance.

Nutrient Uptake by Macrophytes:

We used in-stream mesocosms with nutrient additions to determine SRP uptake rates of the macrophytes in the river. The mesocosms were designed from plastic garbage cans by removing the bottoms of the garbage cans. The mesocosms had a radius of 0.25 m. We also drilled two 4-cm diameter holes directly across from each other to allow water flow through the inner chamber. We placed the mesocosms in the stream by lodging them in the soft sediment with an average water depth within of 0.34 m. The mesocosms were left in place overnight, with water flowing through to allow the systems to equilibrate. The next day, we plugged the holes with rubber stoppers. We then added a nutrient solution containing phosphate and a chloride tracer (KH_2PO_4 and NaCl). We calculated the addition volume of nutrient solution for each mesocosm based on the volume of water within the mesocosm. SRP concentrations were raised to approximately two times the ambient stream concentrations.

We carried out the mesocosm procedure twice, 8-7-06 through 8-9-06 and 8-30-06 through 9-1-06. The first experiment was carried out just below Dn 3 and the second experiment was carried out just above Up 1. Each experiment was comprised of two treatments, one containing macrophytes and one serving as a control with no macrophytes. Each treatment had four replicates. Each replicate was sampled at the initial placement of the mesocosms, directly before nutrient addition, and at times t_0 , t_2 , t_4 , t_6 , and t_{24} , where subscripts refer to hours after nutrient addition (t_0 was directly after the addition). We sampled using the same technique as in the nutrient sampling of the distributional study. SRP was analyzed as described above. Chloride samples were frozen and analyzed at a later date using a Dionex ion chromatograph.

We obtained uptake rates for each treatment group using nutrient spiraling theory, substituting time for distance. SRP concentrations were corrected for dilution in the mesocosm by using the dilution of our chloride tracer. The log of the corrected SRP concentration was plotted against time. The slope of the resulting line was S_w , and we used this value to calculate a rate of phosphorus uptake for each mesocosm. Only data from t_0 , t_2 , t_4 , and t_6 were used because of an unexpected massive release of SRP overnight, which was captured in virtually all of the t_{24} samples. One control replicate from the second experiment had to be discarded due to disruption of the mesocosm midway through the experiment.

We estimated the uptake of macrophytes in Big Spring per day during the growing season, using an average of 14.7 h daylight/day from May to August. We assumed that macrophytes take up SRP during this time but at no other time of day. We also estimated the impact SRP uptake by macrophytes might make on total SRP flux in Big Spring using sites Up 1 and Dn 2. Using discharge data from an accompanying study and nutrient data from the distributional study, we calculated the average daily SRP flux at Up 1 and Dn 2 for each survey

month. We then calculated what percent of the daily SRP flux the macrophytes had the ability to take up. All data analysis was performed using Sigma Plot (version 9.0, Systat Software Inc.), Sigma Stat (version 3.0, Systat Software Inc.), and Microsoft Office Excel.

Results:

Biomass:

Average biomass in Big Spring throughout the entire study ranged from 4.20 g/m² at Dn 2 to 48.93 g/m² at Up 1 (Figure 2). Average biomass for the whole stream ranged from 1.49 g/m² to 60.32 g/m² in July. Biomass stream-wide peaked in July both years (Figure 3). The decrease in cover through August and September was accompanied by apparent senescence of the macrophytes. By the end of September, most of the plants that remained appeared to be less vigorous than the plants observed in July. By the end of November and early December most of the plants had died. A few persisted into the winter, but the coverage was sparse (<5%) when it did occur, and the persistent plants were small in stature. Plant growth resumed in late March and early April. Plant biomass temporal patterns were consistent between years as well as between reaches above and below the dam (Figure 4).

In the upstream reach, biomass was dominated by *Nitella* and *Z. dubia*. The downstream reach was dominated by *P. crispus* and *Z. dubia* (Figure 5). *P. crispus* is an invasive species that reproduces vegetatively through dormant apices (Nichols and Shaw, 1986). The dam in the midst of our study site may block the spread of *P. crispus* to the upstream reach, which explains in part the difference in species composition between the upstream and downstream reaches.

Distribution:

We found that all of the sites had significantly different below-canopy PAR (ANOVA, $N=15$, $F=17.931$, $P<0.001$). Upstream and downstream sites did not differ significantly in their SRP concentrations (t-test, $P>0.05$). The best predictor of macrophyte distribution was below-canopy PAR, which accounted for 80.36% of variation in macrophyte abundance among sites (Figure 6). At some sites, water-column nutrient concentrations also correlated with macrophyte distribution, but these correlations were negative. Nitrate (NO_3^-) concentrations correlated significantly to biomass at Dn 0, Dn 1, and Dn 3. SRP, on the other hand, correlated significantly with biomass only at Dn 1 (Table 2). There was not a significant enough difference between temperature at each site to draw a correlation between temperature and biomass (data not shown). Velocity and biomass were also negatively correlated, with significant relationships at Up 1, Dn 0, Dn 1, and Dn 3 (Table 2).

Some significant relationships were seen between individual species and the parameters tested. *Z. dubia* was the only species in which biomass was significantly correlated with PAR ($P<0.005$). *Z. dubia* biomass was also significantly correlated with NO_3^- , SRP, and especially velocity at several of the sites. *P. crispus* biomass was also significantly correlated with these parameters at some of the sites, but to a lesser extent than *Z. dubia* (Table 3).

Nutrient Uptake by Macrophytes:

Mesocosms with macrophytes had significantly (t-test two-tailed, $P<0.001$) higher uptake rates than did the control mesocosms with no macrophytes (Table 4). The plant mesocosms took up SRP at a net rate of $364.29 \mu\text{g}/\text{m}^2/\text{day}$. The mesocosms with no plants actually released SRP at a rate of $209.19 \mu\text{g}/\text{m}^2/\text{day}$. The gross uptake rate of the plants was $573.48 \mu\text{g}/\text{m}^2/\text{day}$. We determined the gross rate of uptake for the mesocosms with plants by

adding the average rate of SRP release in the no-plant mesocosms to the average net rate of uptake in the plant mesocosms. The gross uptake rate gave us an upper estimate of the uptake rate, while the net uptake rate gave us a lower estimate. If we attribute the SRP uptake observed in the macrophyte treatments to the macrophyte community within the mesocosms, we can estimate the uptake potential of the macrophytes at our sample reaches. Depending on the amount of biomass at each site, the uptake potential ranged from 410.81 $\mu\text{g SRP/day}$ at Dn 2 to 8123.03 $\mu\text{g SRP/day}$ at Up 1 using the net uptake rate, and from 646.72 $\mu\text{g SRP/day}$ at Dn 2 to 12787.67 $\mu\text{g SRP/day}$ at Up 1, using the gross uptake rate (Figure 7). We had discharge data for Up 1 and Dn 2 and were therefore able to calculate the daily SRP load. From that, we determined what percent of the daily SRP load the macrophytes at these sites are able to take up. Using both the gross and net uptake rates, we estimated uptake at Up 1 to be between 0.0029% and 0.0045% of the daily SRP load. It was even lower at Dn 2, where it was between 0.0001% and 0.0002% (Table 5).

Discussion:

We found that submerged macrophytes are plentiful in Big Spring, with average biomass peaking in July. Average biomass across all sites ranged from 1.49 g/m^2 to 60.32 g/m^2 . The temporal patterns of biomass distribution in Big Spring followed closely those of other rivers around the world, where peak biomass occurred in July (Sprenkle *et al.*, 2004; Madsen and Adams, 1988; Sand-Jensen *et al.*, 1989). The range of biomass in Big Spring was close to that in the Piedmont section of the 6th-order James River, Virginia (Sprenkle *et al.*, 2004), but was much

lower than biomass values cited for Badfish Creek, Wisconsin and for a series of rivers in Denmark (Madsen and Adams, 1988; Sand-Jensen *et al.*, 1989).

The distribution of macrophytes in Big Spring was governed largely by light availability. Highly shaded sites, such as Dn 2, had less than 5 g/m² biomass at their peak, while open sites reached up to 100 g/m² biomass at their peak. The lack of significant positive relationships between biomass and nutrient concentrations suggests that the macrophytes are most limited by light, or that they do not rely on the water column for their nutrients. Light is critical for plants, and is often a major limiting factor in macrophyte distribution in aquatic systems, so it is plausible that this also holds for Big Spring (Lacoul and Freedman, 2006).

Velocity is another important factor cited in the literature as limiting macrophyte distribution. In agreement with previous studies, we found a negative relationship between velocity and biomass (Madsen *et al.*, 2001; Lacoul and Freedman, 2006). The results of our study suggest that the number cited by Madsen *et al.* is more applicable to Big Spring than the numbers cited by Lacoul and Freedman, see above. The average velocity at any given site was never greater than 0.35 m/s, and a negative relationship is clearly visible in our data. However, it is hard to determine the exact nature of the relationship between biomass and velocity in Big Spring. It is well known that macrophyte beds decrease water velocity, and this effect could be what our data illustrates (Madsen *et al.*, 2001; Horvath, 2002; Champion and Tanner, 2000). Instead of high water velocity inhibiting macrophyte production, high macrophyte production could have decreased water velocity. Given the data, it is impossible for us to decouple these two possibilities.

We also examined the effect of water-column nutrient concentrations on macrophyte distribution and production. We expected to see a positive relationship between N and P

concentrations and biomass, because these are critical nutrients that often limit macrophyte production. There was not a significant relationship between N and P concentrations and biomass at most of the study sites. When we did find a significant relationship, it was always a negative correlation. Because of this result, we suspect that the macrophytes at Big Spring are not limited by water-column N and P availability. One explanation of the unexpected negative correlation might be that, since our data stretch across the seasons, there is a seasonal factor that has opposite effects on biomass and nutrient concentrations. Another explanation is that the macrophytes may actually affect N and P concentrations via direct uptake.

The results from the mesocosm experiment support the idea that macrophytes in Big Spring are actually able to decrease N and P concentrations at peak biomass. We found that mesocosms containing macrophytes had an SRP uptake rate significantly larger than that of mesocosms lacking macrophytes. The mesocosms without macrophytes actually released SRP over time. This could be because flow through the mesocosms was restricted throughout the experiment, which may have affected dissolved oxygen levels. Changing DO levels can change redox conditions and result in the release of P sorbed to the sediment. Further studies monitoring oxygen levels in periods of zero-flow conditions are necessary to confirm this theory.

We found that macrophytes in Big Spring have an SRP uptake rate in the range 364.29-573.48 $\mu\text{g}/\text{m}^2/\text{hr}$, which equates to a range of 8.74-13.76 $\text{mg}/\text{m}^2/\text{day}$. This range of uptake values is comparable to many previous estimates of SRP uptake rates by macrophytes (Meals *et al.*, 1999; Pelton *et al.*, 1998). Our range of uptake rate values also falls well below the range of total P retention rates from nutrient spiraling studies (Meals *et al.*, 1999; Ensign and Doyle, 2006).

Each study reach at Big Spring had different daily uptake potential, given that they varied in macrophyte cover. At Up 1 and Dn 2, SRP uptake potential ranged from 0.0029% to 0.0045% and from 0.0001% to 0.0002%, respectively, of the daily SRP load at each site. Up 1 had the highest average biomass, while Dn 2 had the lowest biomass. It is likely, therefore, that these percentages reflect a general range for the entire study reach, assuming that discharge did not vary greatly among the study sites. Pelton *et al.* (1998) estimated, however, that macrophytes and the associated epiphyton in the LaPlatte River, Vermont, take up as much as 4% of the daily SRP load.

Our results agree with previous studies showing that macrophytes have the ability take up and retain nutrients in streams (Meals *et al.*, 1999; Bernot *et al.*, 2006; Pelton *et al.*, 1998; Wade *et al.*, 2002). Some studies, however found that macrophytes did not increase uptake and retention of nutrients. Wilcock and his colleagues (2002) found that nutrient uptake and retention was greater in reaches with low biomass than in reaches with high biomass. They acknowledge the potential for macrophytes to contribute to nutrient retention and cite variation in water velocity as a potential explanation for the differing impacts of macrophytes on retention that they saw.

Macrophyte uptake of SRP must result in long-term storage of P in order to have a large impact on nutrient concentrations in the stream, but there is some evidence in our data that the macrophytes in the mesocosms stored P only in the short-term. After 24 hours, many mesocosms had highly elevated SRP levels. Even mesocosms containing macrophytes, which had taken up SRP in the first six hours of the experiment, showed large releases of SRP overnight. We disregarded these data points in the data analysis because another process was clearly affecting the system. However, the behavior is important in order to determine the

potential impact macrophytes have on nutrient dynamics in Big Spring. Five out of eight macrophyte replicates and four out of seven no-macrophyte replicates exhibited this behavior. Because SRP was released overnight in both treatments, the mechanism is likely not related to macrophytes. It is possible that the mesocosms became anoxic, because water was not flowing through them. The non-macrophyte replicates released SRP throughout the experiment, but the macrophyte replicates shift behavior overnight. They may have remained oxygenated through the day because the macrophytes were photosynthesizing, but once the macrophytes stopped photosynthesizing for the day, the mesocosms could have become anoxic, causing a release of SRP from the sediments. Further studies are needed to resolve this problem. If the macrophytes themselves release SRP overnight, any uptake that occurs during the day is offset.

We have shown that macrophytes can take up SRP from the water column and store it, at least in the short-term. Extrapolating the findings from the mesocosm experiment to the whole stream is, however, somewhat limited by the nature of the mesocosms. The advantage of using *in situ* mesocosms rather than microcosms in the lab is that we do not have to disturb the macrophytes to the same degree, and they remain in their natural habitat. Laboratory microcosms can only mimic the stream environment. The disadvantage to *in situ* mesocosms is that we are limited by technology and are not able to maintain water flow through the mesocosms during the experiment. Because water flow oxygenates the water, removing the flow can result in changes in DO levels. Water flow also decreases the size of the boundary layer surrounding macrophyte leaves. Thinner boundary layers make it easier for macrophytes to take up gases and nutrients from the water column. Thus, we likely underestimated the SRP uptake rate of macrophytes.

Regardless of the limitations to the study, we have evidence that macrophytes have very little affect on water-column nutrient concentrations in Big Spring. Although the negative correlations we saw between ambient N and P concentrations and biomass are highly suggestive that macrophytes decrease ambient nutrient concentrations, our estimates of total uptake potential of macrophytes are less than 0.005% of the daily SRP load in the system. Though there have been many studies suggesting that macrophytes could play a significant role in moderating water chemistry, our data support no such conclusion. What little affect the macrophytes might have had was overridden by the ambient nutrient concentrations in Big Spring.

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Tables and Figures:

Table 1: R² values of percent cover-biomass regressions for each species.

Species	R²
<i>P. crispus</i>	0.689
<i>Z. dubia</i>	0.886
<i>P. Pusillus/foliosis</i>	0.856
<i>E. Canadensis</i>	0.807
<i>Nitella</i>	0.794

Table 2: Regression of SRP, NO₃, and velocity with Biomass for each reach. Dn 0, Up 1, and whole stream were log transformed for SRP regressions to achieve constant variance; whole stream was log transformed for velocity also. Whole stream failed the normality test for SRP and velocity regressions. Bold values represent significant relationships.

Site	Velocity		SRP		NO ₃	
	R ²	P-value	R ²	P-value	R ²	P-value
Up 1	0.6563	0.0025	0.0047	0.8411	0.0620	0.5181
Up 2	0.2636	0.1062	0.0547	0.4889	1.48E-5	0.9922
Dn 0	0.6763	0.0019	0.3323	0.0634	0.6829	0.0032
Dn 1	0.7656	0.0004	0.5292	0.0112	0.6392	0.0055
Dn 2	0.0817	0.3943	0.1666	0.2126	0.1710	0.2349
Dn 3	0.6932	0.0015	0.2673	0.1034	0.8026	0.0005
Whole Stream	0.0751*	0.0260*	0.0667*	0.0363*	0.0176	0.3205

Table 3: Species with significant relationships to velocity, SRP, and NO₃ (P < 0.05). Log transformations were used as necessary to achieve constant variance.

Site	Velocity	SRP	NO ₃
Up 1	<i>Z. dubia</i>	<i>Z. dubia</i>	---
Up 2	<i>Z. dubia</i>	---	---
Dn 0	<i>E. Canadensis</i>	---	<i>P. crispus</i>
	<i>P. crispus</i>		<i>Z. dubia</i>
	<i>Z. dubia</i>		
Dn 1	<i>P. pusillus/foliosus</i>	<i>P. crispus</i>	---
	<i>Z. dubia</i>		
Dn 2	---	---	---
Dn 3	<i>P. crispus</i>	---	<i>P. crispus</i>
	<i>Z. dubia</i>		<i>Z. dubia</i>
Whole Stream	<i>Z. dubia</i>	<i>P. crispus</i>	---
		<i>Z. dubia</i>	

Table 4: Uptake rate measurements

	No Plant	Net Plant	Gross Plant
\bar{U} ($\mu\text{g}/\text{m}^2/\text{day}$)	-209.192	364.2884	573.4804
n	7	8	N/A
SD	296.6679	199.388	N/A

Table 5: Percent of daily SRP load retained by macrophytes at sites Up 1 and Dn 2.

	Mean daily SRP load (μg)	Mean % uptake of SRP load (gross U)	Mean % uptake of SRP load (net U)
Up 1	361,755,234.1	0.0029	0.0045
Dn 2	457,777,526.4	0.0001	0.0002

Figure Captions:

Figure 1: Map of the study reach, indicating the location of each site.

Figure 2: Average biomass at each site after 2 years of sampling. Error bars represent standard error.

Figure 3: Average biomass along the study reach through out sampling. Error Bars represent standard error.

Figure 4: a. Average biomass at downstream sites. Error bars = standard error for all sites with 3 or more replicates.

b. Average biomass at upstream sites. Only 2 replicates were used, so standard error was not calculated.

Figure 5: Biomass distribution by species.

a. Upstream

b. Downstream

Figure 6: Regression of below canopy PAR and biomass along all of the study reaches.

$R^2=0.8036$, $p\text{-value}=0.0226$.

Figure 7: SRP uptake potential for each study reach, using both gross and net uptake rates.

Error bars = SE for sites with 3 replicates.

Figure 1

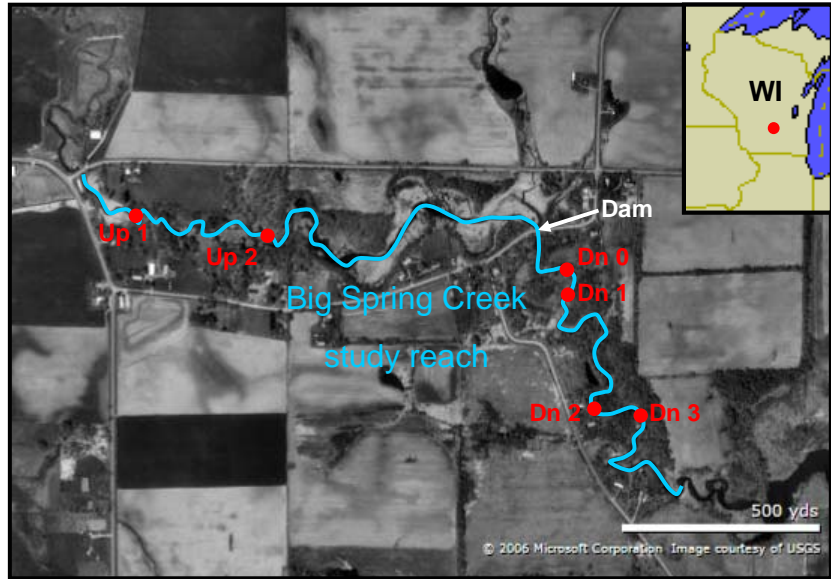


Figure 2

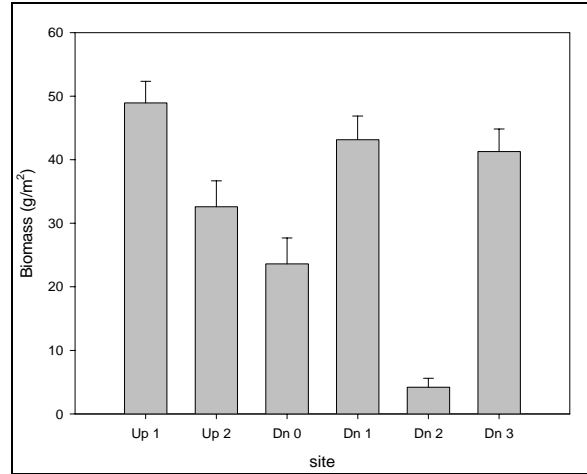


Figure 3

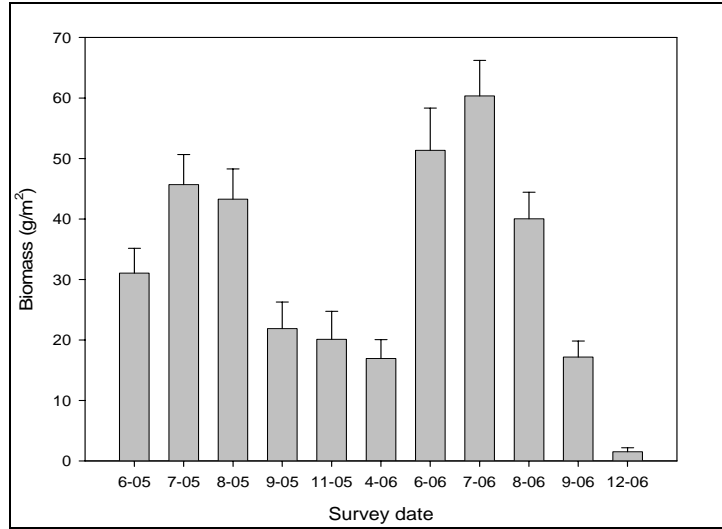


Figure 4

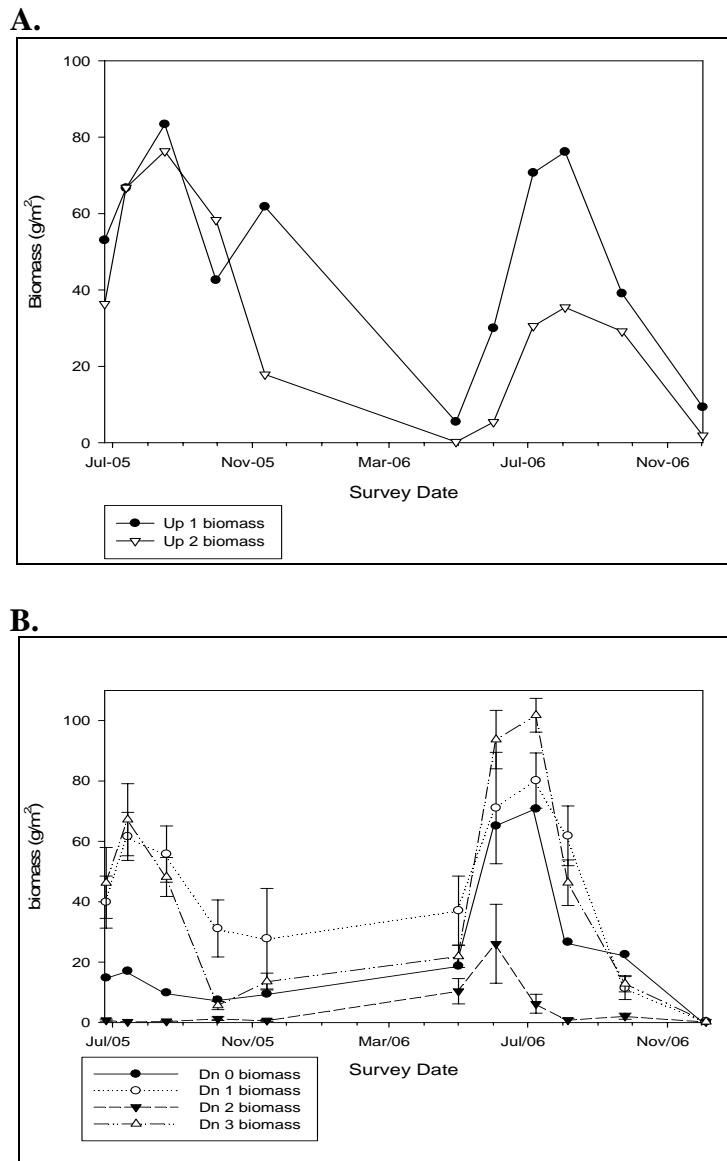
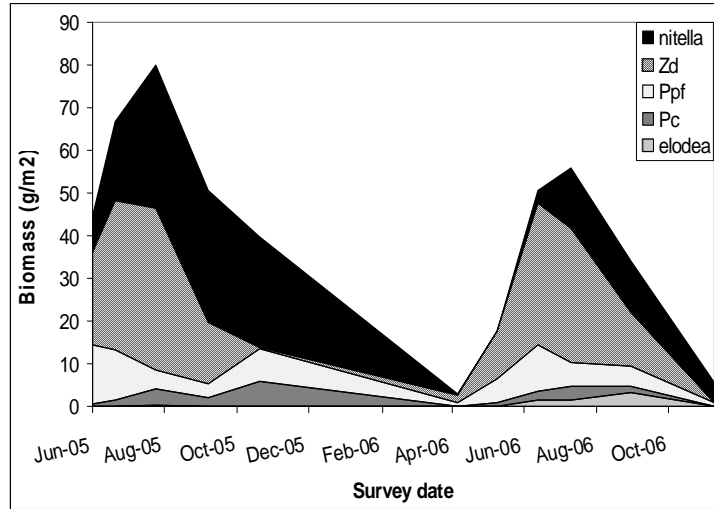


Figure 5

A.



B.

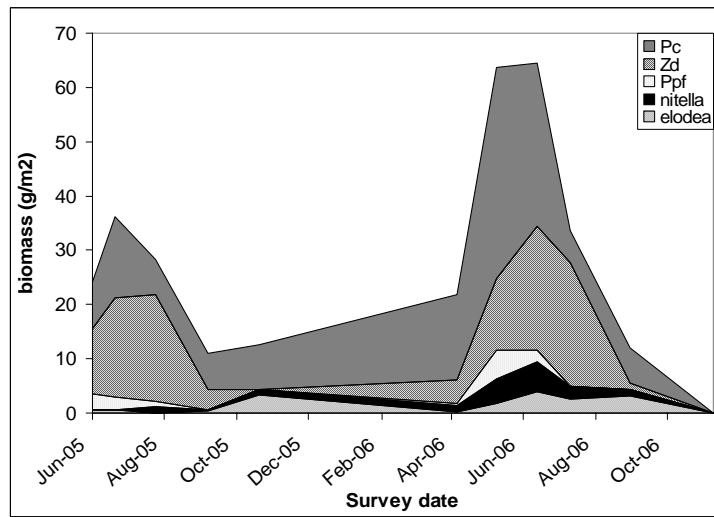


Figure 6

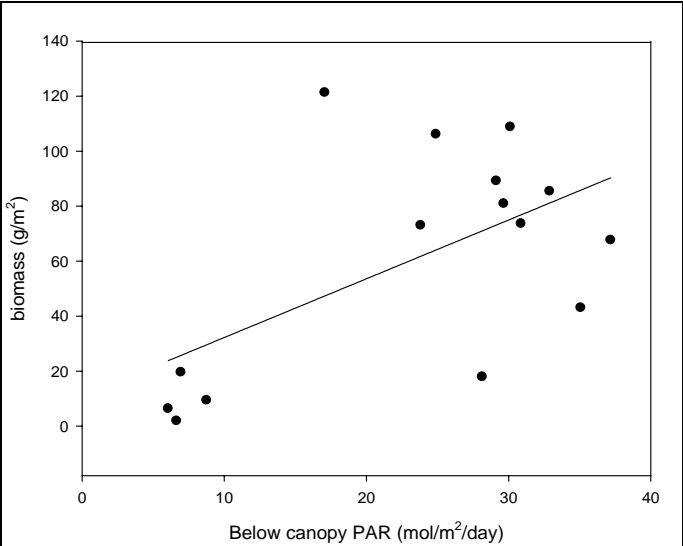


Figure 7

