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ARTICLE

Thresholds in the Response of Free-Floating Plant Abundance to Variation in Hydraulic Connectivity, Nutrients, and Macrophyte Abundance in a Large Floodplain River

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Abstract Duckweed and other free-floating plants (FFP) can form dense surface mats that affect ecosystem condition and processes, and can impair public use of aquatic resources. FFP obtain their nutrients from the water column, and the formation of dense FFP mats can be a consequence and indicator of river eutrophication. We conducted two complementary surveys of diverse aquatic areas of the Upper Mississippi River as an in situ approach for estimating thresholds in the response of FFP abundance to nutrient concentration and physical conditions in a large, floodplain river. Local regression analysis was used to estimate thresholds in the relations between FFP abundance and phosphorus (P) concentration (0.167 mg l^{-1}), nitrogen (N) concentration (0.808 mg l^{-1}), water velocity (0.095 m s^{-1}), and aquatic macrophyte abundance (65 % cover). FFP tissue concentrations suggested P limitation was more likely in spring, N limitation was more likely in late summer, and N limitation was most likely in backwaters with minimal hydraulic connection to the channel. The thresholds estimated here, along with observed patterns in nutrient limitation, provide river scientists and managers with criteria to consider when attempting to modify FFP abundance in off-channel areas of large river systems.

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Introduction

Free floating plants (FFP) are common in aquatic ecosystems and, when conditions are favorable, can form thick surface mats that substantially affect ecosystem processes and condition (Parr and Mason 2004). Such surface mats are often dominated by duckweeds (*e.g.*, *Lemna* spp.) and may contain filamentous algae (*e.g.*, *Cladophora* spp.) and other species. Specific ecosystem effects of abundant FFP can include reductions in the following: dissolved oxygen concentration (Pokorny and Rejmankova 1983), phytoplankton growth rate and abundance (O'Farrell et al. 2009), and zooplankton growth rate and abundance (Fontanarrosa et al. 2010). Abundant FFP have also been associated with increased sediment oxygen demand (Parr and Mason 2004), and increased sediment nutrient release (Boedeltje et al. 2005). In addition, thick mats of abundant FFP can interfere with public recreation (Hall and Cox 1995), provide minimal benefits for invertebrates (Neill and Cornwell 1992), negatively affect fish and wildlife (Parr and Mason 2004), and can reduce submersed aquatic vegetation (SAV) abundance due to reduced light penetration (Portielje and Roijackers 1995; Morris et al. 2003).

Free floating plants are capable of growing and reproducing rapidly under favorable conditions. FFP obtain nutrients solely from the water column, and can respond rapidly to sustained nutrient availability (Landolt and Kandeler 1987). Specifically, elevated phosphorus (P) and nitrogen (N) concentrations have been associated with high FFP biomass (De Groot et al. 1987; Luond 1990; Szabo et al. 2005; Makarewicz et al. 2007). Favorable environmental conditions for FFP include warm water temperature (Landolt and Kandeler 1987), shallow water depth (Janse and Van Puijenbroek 1998), low water velocity (Duffield and Edwards 1981), and low pH (Szabo et al. 2005). Additionally, the presence of rooted aquatic macrophytes (submersed, rootedfloating-leaved, and emergent), which act as a substrate to hold FFP in place, has been associated with high FFP biomass (McDougal et al. 1997).

The concentration of N and P varies spatially and temporally in large floodplain river ecosystems (Knowlton and Jones 1997; Tockner et al. 1999). In the Upper Mississippi River, total N and P concentration tend to decline and increase through the growing season, respectively (Houser and Richardson 2010). During the growing season, N concentration tends to be highest in the main channel and, among backwaters, N concentration tends to be higher in backwaters which are more connected to the main channel (Richardson et al. 2004). Nutrient sediment release is an important source of P input to the water column during the growing season in the Upper Mississippi River (James and Barko 2004; Houser et al. 2013).

Because FFP are dependent on water column nutrient concentrations, it is possible that the spatio-temporal variability in nutrient availability leads to spatio-temporal variability in nutrient limitation of FFP. FFP tissue nutrient concentration and stoichiometry can indicate which nutrients are most likely limiting growth (Sterner and Elser 2002; Klausmeier et al. 2004; Hall et al. 2005; Demars and Edwards 2007). Minimum water column nutrient concentrations required to maintain tissue nutrients, and therefore continuous growth of FFP, have been identified in a laboratory setting (Roijackers et al. 2004 and references therein). Additionally, tissue nutrient ratios can indicate which nutrient can be limiting FFP growth or abundance (Demars and Edwards 2007).

The Upper Mississippi River has experienced severe proliferation of FFP biomass in recent years. As a result, large areas of backwater habitat have been covered by FFP mats, which reduce surface re-aeration and photosynthesis and generate hypoxic conditions (Houser and Richardson 2010). To improve ecosystem function, it is important for river scientists to understand factors driving FFP production in floodplain rivers so management strategies can be developed to prevent the proliferation of these extensive mats.

Because the Upper Mississippi River exhibits extensive variation in nutrient availability, hydraulic connectivity, current velocity, depth, and vegetation abundance, the specific factors limiting FFP abundance likely vary spatially and temporally across the aquatic areas of the floodplain. Thus, the Upper Mississippi River provides a useful system for estimating thresholds in the response of FFP to a suite of chemical and physical factors in a large floodplain river. We address the following questions: 1. Do the changes in nutrient concentrations across gradients of hydraulic connectivity and season result in temporal and spatial patterns in FFP tissue nutrient content and nutrient limitation of FFP? 2. What thresholds can be detected in the relations between FFP biomass, water velocity, water column N and P concentrations, and aquatic macrophyte cover?

Methods

Study Area

The Upper Mississippi River consists of a series of navigation pools extending from Minneapolis, Minnesota to the confluence of the Ohio River at Cairo, Illinois, USA. The navigation dams are low-head dams built to maintain sufficient depth in the river for navigation during the low flow season and were designed to have little impact on discharge or water level during high flow and flood conditions (Sparks 1995). Thus navigation pools are unlike reservoirs in that they remain riverine in nature. The study was conducted in Navigation Pool 8 of the Upper Mississippi River. Pool 8 is located between Lock and Dam 7 (Dresbach, MN, USA) and Lock and Dam 8 (Genoa, WI, USA; Fig. 1). It is 39 km long and encompasses 9,000 aquatic ha. Pool 8, typical of the navigation pools of the Upper Mississippi River, is composed of a diverse array of aquatic areas (Wilcox 1993) and has been stratified for sampling purposes into main channel, side channel, contiguous backwaters, isolated backwaters, and impounded areas (Soballe and Fischer 2004). The main channel is deep and is characterized by relatively high water velocity (0.20–0.60 m s^{-1}). Side channels are lotic but exhibit depth and water velocity that is generally less than that of the main channel. Contiguous backwaters typically exhibit very low water velocity (often below detection) and are connected by surface water to main or side channel habitat at normal river stage. Isolated backwaters typically exhibit undetectable water velocity and lack a surface water connection to channel habitat at normal river stage. The impounded area is the large expanse of open water located directly upstream of the lock and dam. The Upper Mississippi River is highly modified for navigation and is unusual among large rivers in that the contiguous backwaters retain surface water connections to flowing channels even during low flow conditions. More detailed descriptions of these contrasting aquatic areas can be found in Strauss et al. (2004).

Study Design

The study design consisted of two complementary components. The connectivity component consisted of monthly (May–October 2010) sampling at five locations in each of two high connectivity (to the main channel) backwaters (Round and Horseshoe Lakes) and two low connectivity backwaters (Markle and Beiers Lakes) (Figs. 1a and 2a). Data from the connectivity component were used to describe

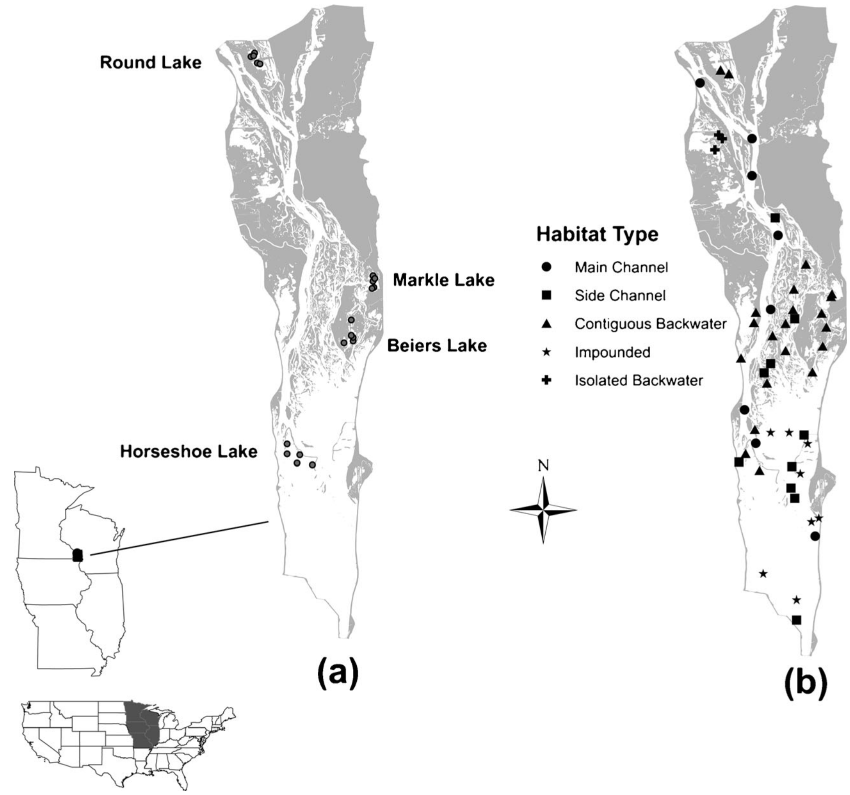

Fig. 1 Location of sampling sites within Navigation Pool 8 of the Upper Mississippi River for **a** the connectivity sampling component, and **b** stratified random sampling (SRS) component. *Grey* indicates land, white indicates water

temporal trends and estimate thresholds for FFP biomass response. All statistical analyses were conducted using the connectivity component data unless otherwise stated.

The stratified random sampling component consisted of 50 sites distributed across main channel (n=8), side channel (n=10), impounded (n=8), contiguous backwater (n=21), and isolated backwater (n=3) strata that were sampled during a 2-week period beginning the last week of July (Figs. 1b and 2a). The data from this design were collected as ancillary data in conjunction with routine data collection by the U.S. Army Corps of Engineers' Upper Mississippi River Restoration-Environmental Management Program-Long Term Resource Monitoring Program element. The stratified random sampling sites spanned a broad range of hydraulic connectivity, but were restricted in temporal extent. The differences among sample sizes for different strata resulted from a compromise between the portion of Pool 8 encompassed by that strata and variability within the strata (i.e. more limnological variability exists among the contiguous backwaters than within the main channel). Data from the stratified random sampling component were used to test the threshold estimates derived from the connectivity component data.

Water Sampling

Water samples were taken at a depth of 0.20 m at each site to assess water column total nitrogen (TN) and total phosphorus (TP). TN and TP samples were preserved in the field with concentrated H_2SO_4, transported on ice, and refrigerated until analysis. TN and TP concentrations were determined colorimetrically using standard methods (APHA 1992). Measurements of water depth and water velocity (Marsh-McBirney, model 2000, Flo-Mate, Frederick, MD, USA) were collected at each site. Water temperature measurements were taken at 0.20 m using a multiparameter sonde (Minisonde MS5, Hach Company, Loveland, CO, USA). Discharge data were collected by the U.S. Army Corps of Engineers at Lock and Dam 8, Genoa, WI, USA (www.mvp-wc.usace.army.mil). Further details regarding field methods can be found in Soballe and Fischer (2004).

Free-Floating Plant Biomass and Aquatic Macrophyte Cover Sampling

FFP samples for the determination of biomass, dominant taxa and tissue C, N and P content were collected from a 0.25 m^2 quadrat on a randomly selected side of the boat (center-starboard, center-port) at each sampling site. The dominant FFP taxon of the sample was recorded based on visual inspection. Dry weight biomass (g m^{-2}) was determined by drying the FFP samples at 80 °C for 48 h and weighing. FFP samples were then ground with a Wiley Mill (Thomas Scientific, Swedesboro, NJ, USA) to pass a 1 mm sieve and then further ground in a ring and puck grinder to pass a 100 mesh sieve (0.15 mm) and analyzed for C, N and P concentrations. A LECO CNS-2000 analyzer (St. Joseph, MI, USA) was used to

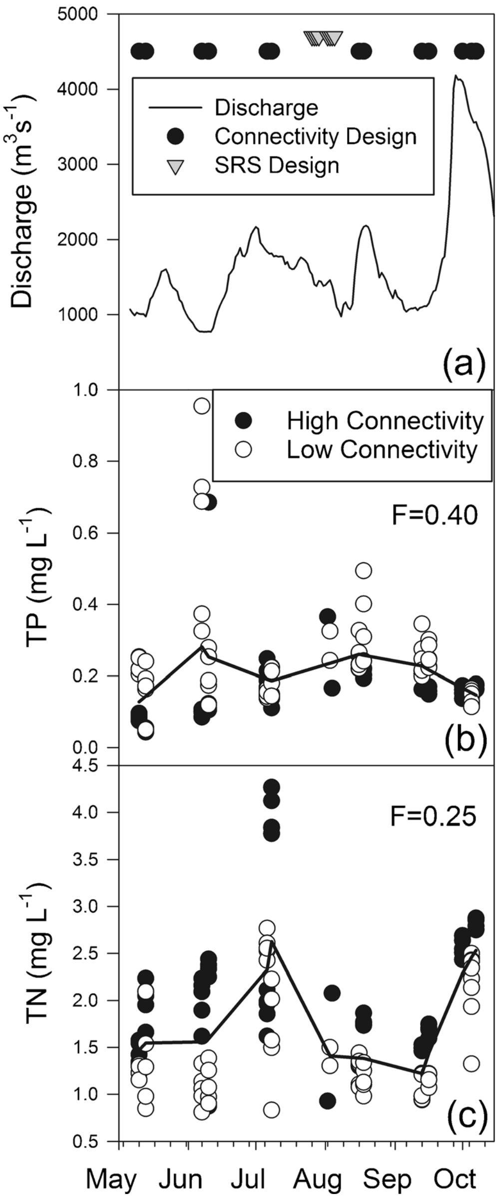

Fig. 2 **a** Discharge (m^3 s^{-1}) at Lock and Dam 8 during the sampling period. The symbols represent sampling days for the connectivity and stratified random sampling components. **b** Water column total phosphorus concentration at high and low connectivity backwater sampling sites by date from the connectivity sampling component. The *solid line* indicates the LOESS regression trend with individual smoothing parameter (F) and **c** water column total nitrogen

analyze FFP C and N by dry combustion with infrared detection of CO_2 plus thermal conductivity detection of N_2 in combustion gases. FFP tissue P concentration was analyzed as part of the total mineral analysis. Total mineral analysis included the digestion of the plant material in concentrated nitric acid with heating at 120–130 °C for 14 h followed by further digestion with two cycles of 0.5 mL of 30 % hydrogen peroxide with heating to 120–130 °C for 30 min and final dilution to 50 mL. The determination of the elements in the diluted digest was performed using a Thermo Jarrel Ash IRIS Advantage ICP-OES (Inductively Coupled Plasma Optical Emission Spectrometry; Franklin, MA, USA). FFP tissue and water column nutrient ratios (N:P, C:N, C:P; by moles) were determined as molar ratios.

Aquatic macrophyte cover at each site was estimated visually (to the nearest 5 %) for the area within 25-m of the boat. Cover was estimated separately for rooted floating-leaved, emergent, and SAV aquatic macrophyte life forms and then summed to generate an aquatic macrophyte score (Yin et al. 2000). It was possible for all three macrophyte life forms to overlap, therefore total cover score sometimes exceeded 100 %.

Backwater Connectivity

An index of backwater connectivity (connectivity score) was developed using water velocity data from the summer, fall and winter from 1993 to 2008 that was collected by the Upper Mississippi River Restoration- Environmental Management Program-Long Term Resource Monitoring Program. Mean water velocity for each backwater was used as an indicator of backwater connectivity (Horseshoe Lake, mean velocity= 0.112 m s^{-1}, n=102; Round Lake=0.048 m s^{-1}, n=48; Markle Lake=0.014 m s^{-1}, n=35; Beiers Lake=0.008 m s^{-1}, n=53).

Statistical Analyses

Spearman rank correlation (R_s) was used to assess the relations between water column and FFP tissue nutrient concentrations and ratios and to describe temporal trends (correlation with day of year) in nutrient concentrations and ratios through the growing season as described by Rodrigues and Williams (2002). Non-parametric Mann-Whitney rank sum tests were used to evaluate differences in water column and FFP tissue N and P concentration among the high and low connectivity backwaters. Thresholds in the relations between FFP abundance and various covariates were estimated using a nonparametric method for estimating local regression surfaces (PROC LOESS; SAS 9.2, 2008). The regression smoothing parameter was generated by default in SAS to strike a balance between residual sum of squares and the complexity of the fit. The PROC LOESS output was used to detect abrupt breakpoints, or thresholds, in the relations between selected variables. Once the thresholds were identified, linear or nonlinear regression was performed to estimate the x-axis intercept for select environmental variables.

Results

Seasonal Patterns in Discharge, Nutrients, and FFP Biomass

Discharge was characterized by three spring and summer peaks followed by a major flood event in late-September into early-October (Fig. 2a). P concentration was variable over the growing season with notably high concentrations occurring in June (Fig. 2b). N concentration peaked in July, decreased from July–September, and increased again in October in association with the fall flood (Fig. 2c).

There were significant temporal trends in FFP biomass and tissue nutrient concentration and ratios through the growing season. Median (across all sites) FFP biomass was very low in late-spring and early-summer, reached a maximum in August, declined in September and disappeared in October as a result of fall flooding (May, 0 g dry mass m^{-2}; June, 3.45; July, 11.39; August, 46.79; September, 10.57; October, 0). Tissue P increased (R_s= 0.57, n=74, P<0.001) and tissue N decreased (R_s=−0.37, n=74, P=0.001) during the growing season at sites where sufficient FFP biomass was collected (~60 % of sites) to measure tissue nutrient concentrations (Fig. 3). Tissue N:P (R_s=−0.68, n=74, P<0.001) (Fig. 4a) and tissue C:P (R_s= −0.47, n=74, P<0.001) (Fig. 4b) decreased during the growing season. Tissue C:N, increased, albeit weakly, during the growing season (R_s=0.41, n=74, P<0.001) (Fig. 4c). Tissue N:P ratios generally indicated an excess of P relative to N by the criteria developed for aquatic angiosperms (N:P<24:1) (Demars and Edwards 2007).

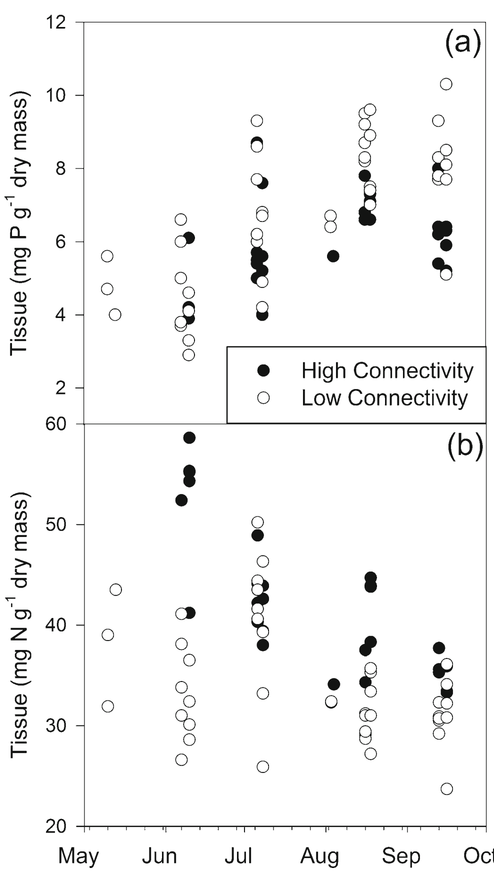

Fig. 3 **a** Free-floating plant (FFP) tissue phosphorus and **b** nitrogen concentration by date from the connectivity sampling component

N:P ratios high enough to suggest P limitation were only observed in the highest connectivity backwater during June (Fig. 4a).

Connectivity, Nutrients, and FFP Biomass

Median water column P concentrations were higher in the low connectivity backwaters (0.22 and 0.163 mg l^{-1} in the low and high connectivity backwaters, respectively) (Fig. 2b); the distributions of the two groups differed significantly (Mann-Whitney test, T=2997, n_1=n_2=62, P<0.001). Median N concentrations were lower in the low connectivity backwaters (1.293 and 1.88 mg l^{-1} in the low and high connectivity backwaters, respectively) (Fig. 2c); the distributions of the two groups differed significantly (Mann-Whitney test, T= 4851.5, n_1=n_2=62, P<0.001).

There were significant correlations between water column nutrient concentrations and FFP tissue nutrient concentrations and ratios. Tissue P was positively correlated with water column TP (R_s=0.30, n=74, P=0.01) (Fig. 5a). Tissue N was positively correlated with water column TN (R_s=0.65, n=74, P<0.001) (Fig. 5b). Tissue N:P was significantly correlated with both water column TP (R_s= −0.49, n=74, P<0.001) (Fig. 5c) and TN (R_s=0.37, n=74, P=0.001) (Fig. 5d). Tissue samples were generally dominated by duckweed species (>90 % of samples). Dominant taxa observed among the tissue samples included: *Lemna minor* (n=35), *Spirodela polyrhiza* (n=23), *Lemna trisulca* (n=7), *Wolffia columbiana* (n=3), *Cladophora* sp. (n=5), and *Spirogyra* sp. (n=1).

There were substantial trends in FFP biomass and tissue nutrient concentrations and ratios across the connectivity gradient most likely reflecting differences in water column nutrient availability across the connectivity gradient. FFP biomass was notably lower in the two higher connectivity backwaters compared to the two lower connectivity backwaters (Fig. 6). Median tissue P concentrations were lower in the high connectivity backwaters (7.0 and 5.9 mg P g^{-1} in the low and high connectivity backwaters, respectively) (Fig. 3a); the distributions of the two groups differed significantly (Mann-Whitney test, T=975, n_1=31 n_2=43, P=0.04). Median tissue N concentrations were higher in the high connectivity backwaters (32.3 and 40.3 mg N g^{-1} in the low and high connectivity backwaters, respectively) (Fig. 3b); the distributions of the two groups differed significantly (Mann-Whitney test, T=1572, n_1=31 n_2= 43, P<0.001). Low N:P ratios, suggestive of N deficiency, were observed more often in low connectivity backwaters and high N:P ratios (>24:1), suggestive of P deficiency, were observed more often in high connectivity backwaters (Fig. 7).

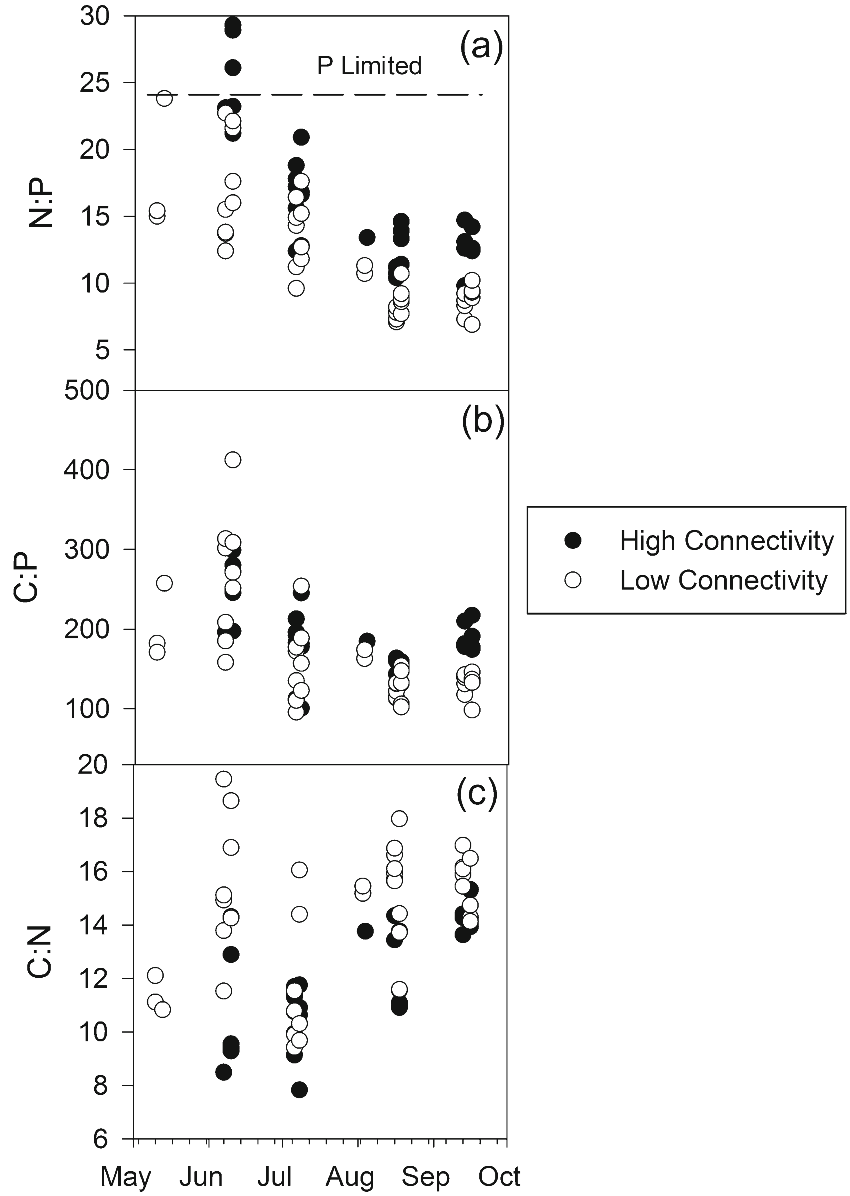

Fig. 4 **a** Free-floating plant (FFP) tissue N:P by date from the connectivity sampling component. Values above the dashed line are suggestive of P limitation for aquatic angiosperms (Demars and Edwards 2007; critical N:P value 24:1). **b** FFP tissue C:P by date from the connectivity sampling component. **c** FFP tissue C:N by date from the connectivity sampling component

Thresholds for FFP Biomass Response to Environmental Conditions

Thresholds were detected in the relations between FFP and water column TP, water column TN, water depth, water velocity, and aquatic macrophyte cover. FFP biomass increased gradually from 0.043 mg l^{-1} to a threshold at 0.167 mg l^{-1} TP above which biomass increased rapidly until TP concentration reached 0.25 mg l^{-1} (Fig. 8a; Table 1). Above 0.25 mg l^{-1} TP, FFP biomass declined with increasing TP concentration. FFP biomass increased gradually as TN concentration increased from 0.808 mg l^{-1} (minimum observed in this study) to 1.308 mg l^{-1} (Fig. 8b). Above this threshold, FFP biomass decreased with increasing TN concentration. The absence of TN values below 0.808 mg l^{-1} prevented the calculation of the x-axis intercept using the LOESS procedure. Although the x-axis intercept is below 0.808 mg l^{-1}, a precise estimate could not be calculated due to limitations in the data distribution.

No thresholds were detected in the relation between FFP biomass and water temperature, and the estimated x-axis intercept was 13.14 °C (Fig. 8c). The fitted relation between water depth and FFP biomass peaked at 1.52 m (Fig. 8d). The fitted relation between water velocity and FFP biomass exhibited a steep negative slope from 0 to 0.095 m s^{-1}, reflecting that most sites with detectable FFP exhibited water velocities of about 0 m s^{-1}; at sites where water velocity was greater than 0.095 m s^{-1}, FFP biomass was nearly always 0 (Fig. 8e).

The fitted relation between FFP biomass and aquatic macrophyte cover exhibited two thresholds (Fig. 8f). From minimal

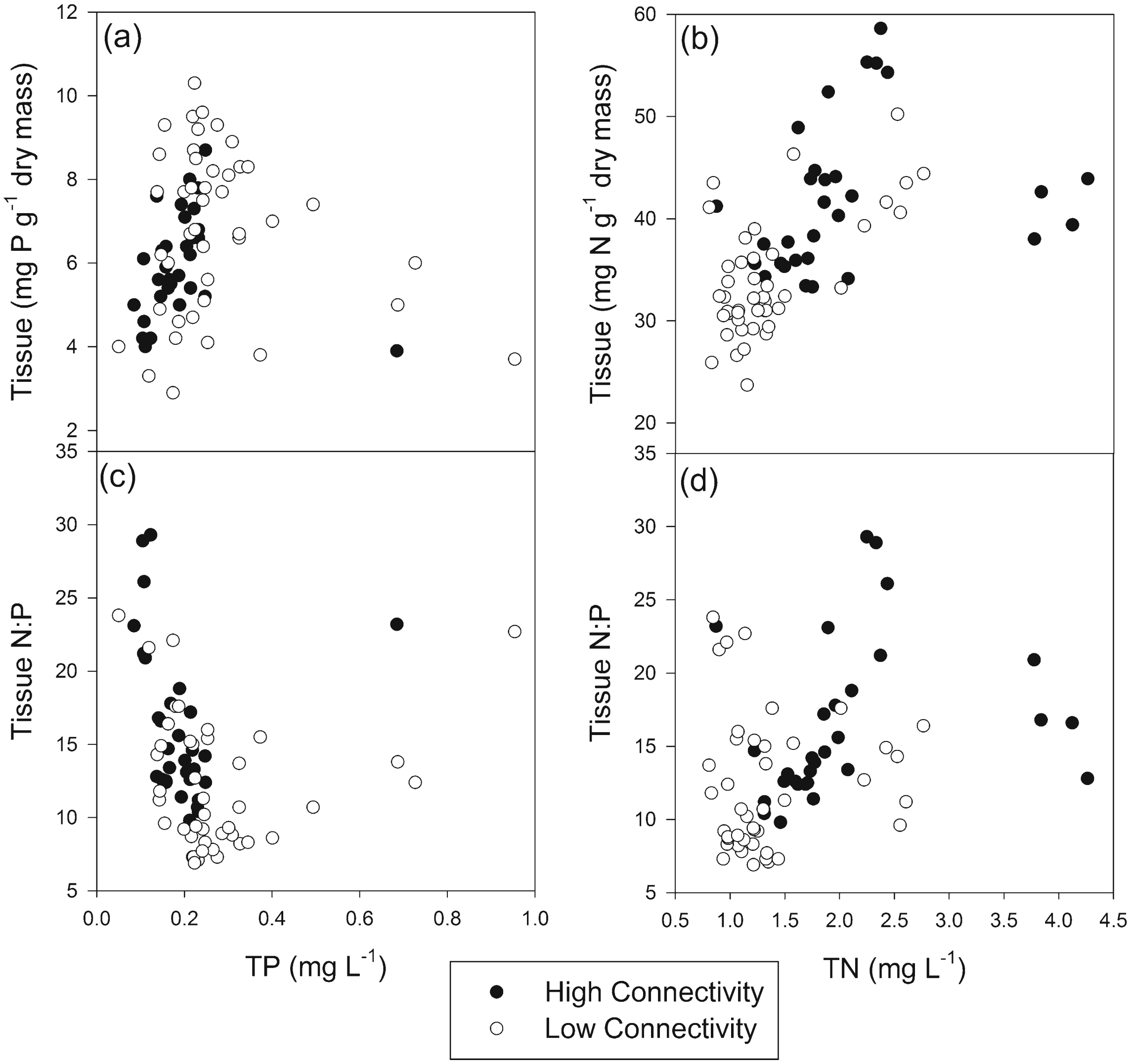

Fig. 5 **a** Relation between free-floating plant (FFP) tissue phosphorus concentration and water column total phosphorus concentration. **b** Relation between FFP tissue nitrogen concentration and water column total nitrogen concentration. Relation between FFP tissue N:P and water column **c** total phosphorus and **d** total nitrogen. All data from the connectivity sampling component

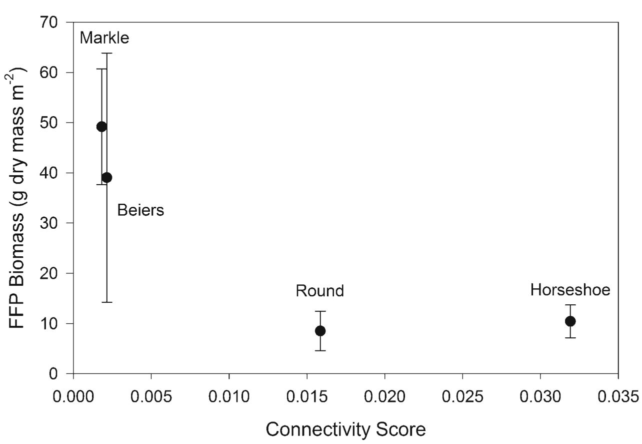

Fig. 6 Mean free-floating plant (FFP) biomass by backwater from the connectivity sampling component. A lower connectivity score indicates less connection to the main channel. Error bars represent +/− one standard error

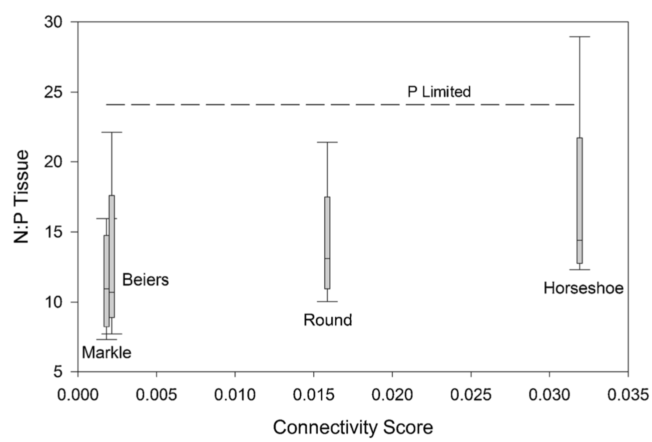

Fig. 7 Box plot of free-floating plant (FFP) tissue N:P by backwater connectivity. A lower connectivity score indicates less connection to the main channel. Values above the dashed line are suggestive of P limitation (Demars and Edwards 2007). *Box plots* represent the 10th, 25th, 50th, 75th and 90th percentiles

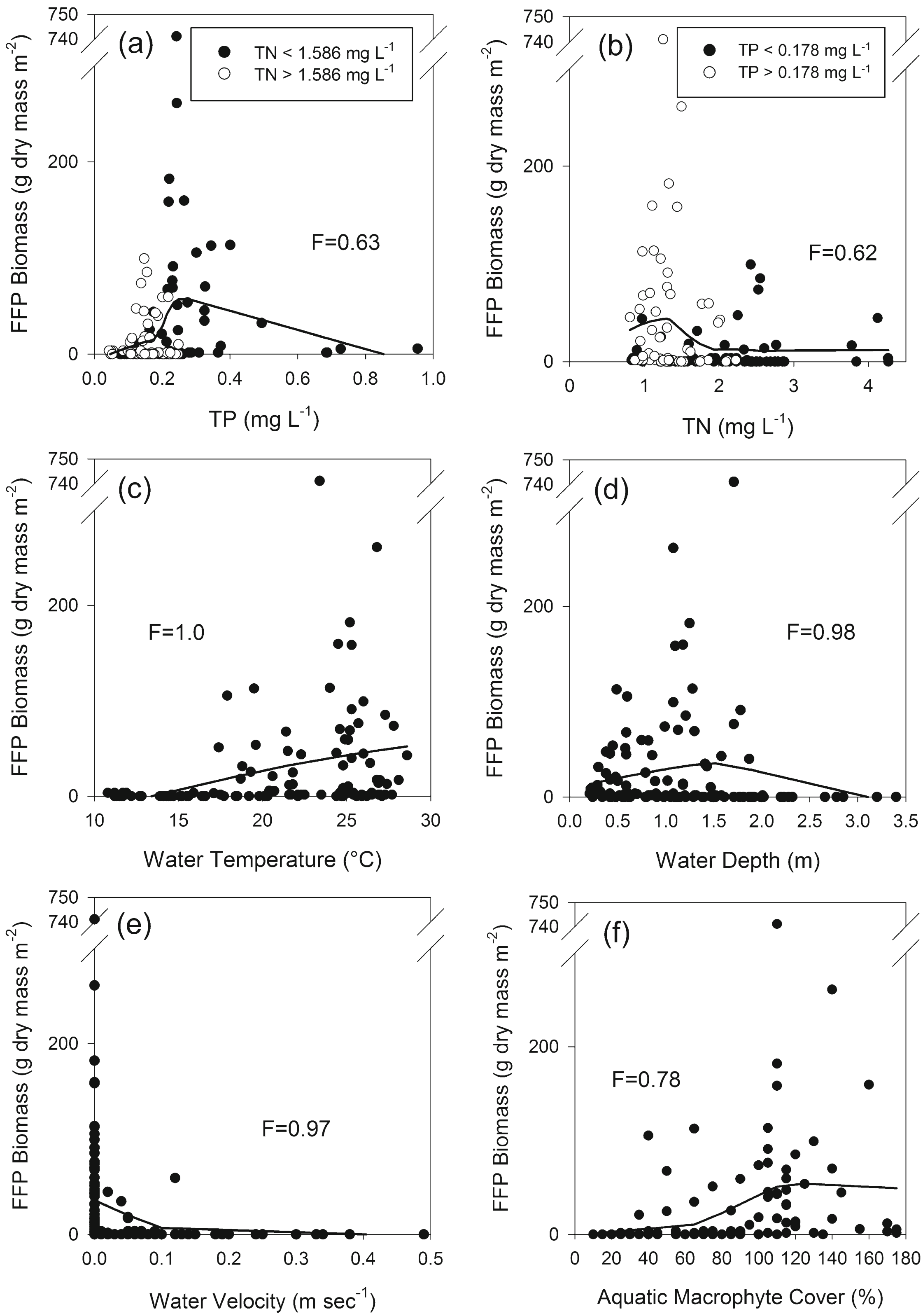

Fig. 8 **a** Relation between free-floating plant (FFP) biomass and total phosphorus concentration from the connectivity sampling component. *Closed circles* represent sites at which total nitrogen was below the median. *Open circles* represent sites at which total nitrogen was above the median. The *solid line* indicates the LOESS regression trend with individual smoothing parameter (F) indicated for each covariate. **b** Relation between FFP biomass and total nitrogen concentration. *Closed circles* represent sites at which total phosphorus was below the median. *Open circles* represent sites at which total phosphorus was above the median. Relation between FFP biomass and **c** water temperature, **d** water depth, **e** water velocity, and **f** aquatic macrophyte cover

cover to 65 % cover there was a gradual increase in FFP. From about 65 % to 110 % cover, FFP biomass increased more rapidly as macrophyte cover increased. Above 110 % macrophyte cover, FFP biomass was highly variable among sites.

The thresholds derived from the connectivity component were tested using the data from the stratified random sampling component. The main channel and side channel sampling strata exhibited lower FFP biomass than the impounded, contiguous backwater and isolated backwater sampling strata (Fig. 9). The main channel and side channel strata exhibited mean velocities above the upper threshold of 0.095 m sec^{-1}, and exhibited aquatic macrophyte cover below the lower threshold of 65 % cover indicating that velocity and macrophyte cover conditions were unfavorable for high FFP biomass. Conversely, the impounded, contiguous backwater and isolated backwater strata exhibited water velocity below the upper threshold and macrophyte cover above the lower threshold indicating favorable water velocity and macrophyte cover conditions for FFP in these strata. Mean nutrient concentrations were greater than estimated minimum threshold in all strata.

Discussion

The spatial and temporal variability typical of large floodplain river ecosystems was reflected in the temporal and spatial patterns of water column and FFP tissue nutrient concentrations observed in this study. There was evidence of P limitation during June when FFP tissue N:P ratios greater than N:P>24:1, the threshold suggested for P limitation in aquatic angiosperms by Demars and Edwards (2007), were occasionally observed. During July, nearly all of the tissue samples suggested surplus N and P relative to criteria determined for aquatic angiosperms (Demars and Edwards 2007 and references therein) and nutrient concentrations were generally high. Elevated water column N concentrations were likely due to relatively high discharge conditions. Elevated water column P concentrations likely resulted from anoxic sediment P release which has been observed to be substantial in the Upper Mississippi River during warm mid-summer conditions (James et al. 1995; Houser et al. 2013). Tissue N:P declined and tissue C:N increased through August and September suggesting that N limitation might be more common in late summer and fall compared to spring. All of the observations suggesting P limitation occurred in high connectivity backwaters, whereas the lowest N:P ratios occurred in the low connectivity backwaters largely due to the low water column N concentration that occurred there.

We detected thresholds in the relations between FFP biomass and TP, TN, depth, water velocity, and aquatic macrophyte cover. Our finding of increasing FFP biomass up to 0.25 mg l^{-1} TP is consistent with the observation of De Groot et al. (1987) who suggested that phosphate is often limiting when water column concentrations are below 0.2 mg l^{-1}. Our finding of decreasing biomass with increasing P concentration above 0.28 mg l^{-1} was an unexpected result. A plausible explanation is that the majority of the observations on the right descending limb of the plot (TP>0.28 mg l^{-1}) occurred at sites with relatively low TN concentrations suggesting N limitation might explain the lower FFP biomass at these sites. These high TP and low TN concentrations often occurred in low connectivity backwaters later in the growing season. Such conditions can result from persistent denitrification, high biotic N uptake, (Richardson et al. 2004; James et al. 2008) and high rates of P release from the sediments (James et al. 1995).

Table 1 Relation between free-floating plant (FFP) biomass and environmental variables (*n*=124 for all tests) during the connectivity sampling component. Range indicates the range of values which can be used to apply the corresponding regression (equation) for estimating FFP biomass. Threshold represents the value of regression breakpoints. Threshold values with lower and upper designations indicate the lower and upper boundaries of the zone of rapidly increasing FFP biomass. The x-axis intercept value indicates where the regression line intersects the x-axis

Dependent variable	Independent variable	Range	Equation	Threshold	X-axis intercept
FFP biomass	TP (mg L^{-1})	0.043–0.167 0.168–0.25	y=−4.959+(116.459×TP) y=−90.233+(606.909×TP)	0.167- lower 0.25- upper	0.043
	TN (mg L^{-1})	0.808–1.308	y=(−40.656×TN^2)+(108.84×TN)−29.1	0.808- lower 1.308- upper	<0.808
	Temperature (°C)	10.8–28.6	y=−47.162+(3.590×Temperature)	None	13.14
	Water depth (m)	0.21–1.52	y=11.202+(17.059×Water Depth)	1.52	3.12
	Water velocity (m s^{-1})	<0.1 >0.1	y=35.751−(302.420×Water Velocity) y=9.031−(22.350×Water Velocity)	0.095	0.405
	Aquatic macrophyte cover (%)[a]	10–65 70–110 115–125 130–175	y=−0.852+(0.175×Macrophyte Cover) y=−0.852+(0.175×Macrophyte Cover) y=27.092+(0.216×Macrophyte Cover) y=66.608−(0.0999×Macrophyte Cover)	65- lower 130- upper	4.85

[a] Sum of percent submersed, rooted floating and emergent macrophyte cover at site

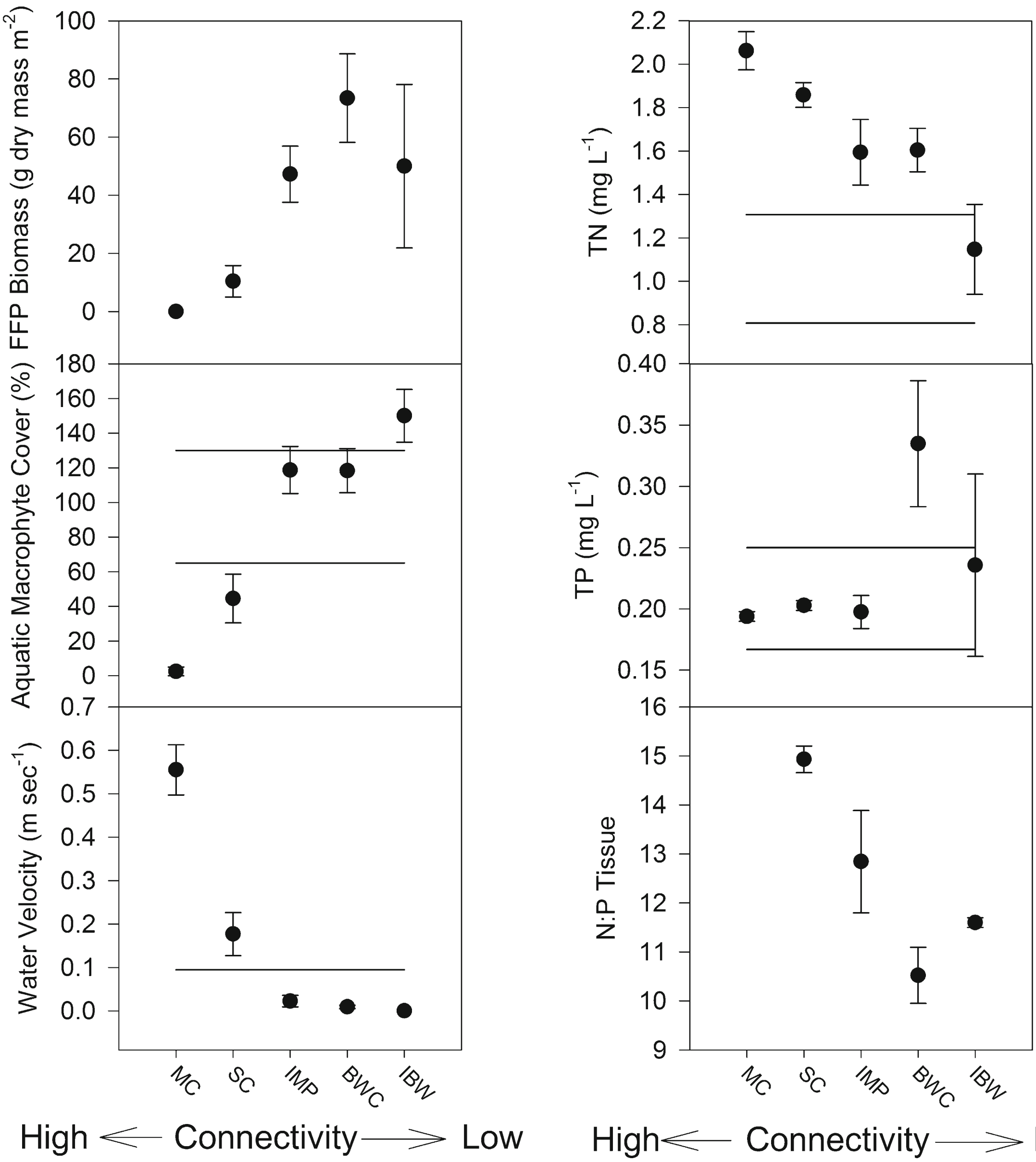

Fig. 9 Mean free-floating plant (FFP) biomass, aquatic macrophyte cover, water velocity, water TN concentration, water TP concentration, and FFP tissue N:P by habitat type from the SRS sampling component. The *solid lines* represent thresholds developed using data from the connectivity design. Error bars represent +/− one standard error

The x-intercept for the relation between water column nutrient concentration and FFP biomass can be interpreted as the minimum required concentration for FFP biomass sustainability (Landolt and Kandeler 1987). The lower x-intercept for water column TP was 0.043 mg l^{-1} similar to the 0.03 mg l^{-1} threshold for minimal FFP growth suggested by Roijackers et al. (2004 and references therein).

In other studies, waters with high N concentration tend to exhibit high FFP biomass and growth rates (Landolt and Kandeler 1987; Szabo et al. 2010). We found biomass increased with water column TN up to 1.308 mg TN l^{-1} and declined above this concentration. Examination of the data on the descending limb of the fitted line (TN>1.308 mg l^{-1}) revealed that the majority of these data points occurred at sites where the TP concentration was relatively low suggesting these sites might have been P limited. The exact x-axis intercept could not be estimated due to limitations in the data distribution. However, visual inspection of the trendline does suggest the value is substantially below 0.808 mg l^{-1}, which appears to be consistent with the concentration required for minimal FFP growth (0.22 mg l^{-1} TN) suggested by Szabo et al. (2005 and references therein).

Physical conditions such as water velocity, water depth and wind and wave action are important in determining FFP distribution (Scheffer et al. 2003), and we detected significant thresholds for several physical variables. We observed a water velocity threshold of 0.095 m sec^{-1}, above which FFP were rarely found. This is similar to the findings of Duffield and Edwards (1981) who reported that water velocity less than 0.1 m sec^{-1} is required for the accumulation of FFP biomass. Wind and wave action can also affect FFP abundance (Boedeltje et al. 2001; Scheffer et al. 2003). Heavy wind and wave action due to the large fetch in the impounded area of our study reach might partially explain why FFP biomass was less abundant in that area relative to that of protected backwaters.

Water depth and its effect on macrophyte cover can influence FFP plant abundance. Maximum FFP biomass was observed at sites with a depth of approximately 1.5 m in our study. Duckweed is known to grow more vigorously in shallow water due to elevated P concentrations near the sediment-water interface (Landolt and Kandeler 1987). The range of aquatic macrophyte cover with the greatest rate of FFP biomass increase (65–110 % cover; Fig. 8f) coincided with depths of 1.5–2.25 m, which approximates the zone of SAV growth in the Upper Mississippi River (Moore et al. 2012). The lower FFP biomass values at depths >2 m are associated with lower SAV abundance and may reflect a lack of physical structure provided by SAV, which could be important during periods of high wind. Lower FFP biomass at sites <1.5 m may have been the result of emergent macrophyte shading (Peck and Smart 1986).

These results indicate that the strong differences in the physical environment (current velocity and macrophyte abundance) between channel and off-channel areas likely explains the high contrast in FFP abundance between these two types of hydrologic regimes, whereas differences in nutrient availability may explain the smaller differences in FFP among off-channel areas. The main channel and side channel sampling strata exhibited FFP biomass far below that of the impounded, contiguous backwater and isolated backwater sampling strata. The major differences between the channels and other aquatic areas were water velocity and aquatic macrophyte cover. The main channel and side channel strata exhibited unfavorable water velocities and aquatic macrophyte cover (too high and too low, respectively). The impounded, contiguous backwater and isolated backwater strata exhibited much lower water velocities, and had higher aquatic macrophyte coverage. Among the three off-channel strata, contiguous backwaters exhibited favorable conditions for FFP by nearly all examined criteria and exhibited the highest mean FFP biomass. Specifically, the contiguous backwaters exhibited relatively high TP and TN concentrations, macrophyte cover in the ideal range, and water velocity near zero. The impounded and isolated backwater strata exhibited marginally lower FFP biomass perhaps due to lower N or P concentrations.

There were clear temporal and spatial patterns in the relative availability of N and P corresponding to spatial and temporal variability in potential nutrient limitation. Early in the growing season and in more connected backwaters, N availability was high relative to that of P whereas the opposite was true later in the growing season and in less connected backwaters. Because these differences in water column nutrient availability were reflected in FFP tissue nutrient content, the influence of connectivity on FFP nutrient content is evident. Thus, these results contribute to the growing body of work illustrating that temporal and spatial variability in connectivity to free-flowing channels is an important component of ecosystem processes within the backwaters of floodplain river systems (e.g., Amoros and Bornette 2002).

The thresholds detected here suggest that under certain conditions, small changes in drivers such as water velocity, aquatic macrophytes, and nutrient concentrations can produce relatively large changes in FFP biomass. Increasing depth >1.52 m, increasing water velocity above zero, and reducing aquatic macrophyte cover below 65 % would all likely result in a reduction in FFP biomass. In addition to improving our understanding of the basic ecology of FFP, our results can provide useful insights into how the future management of off-channel areas may reduce the occurrence of mats formed by over-abundant FFP. For example, management actions on the Upper Mississippi River are often designed to manipulate water velocity (e.g., by modifying connections between channel and off-channel areas (e.g., Johnson et al. 1998)) or to facilitate the establishment of aquatic macrophytes (e.g., constructing islands to reduce wind fetch and create shallow, sheltered areas (e.g., Gray et al. 2010)) Furthermore, the estimated TP threshold supports the numeric P criterion of <0.1 mg l^{-1} TP for Wisconsin non-wadeable rivers (Wisconsin Administrative Code NR 102.06(3)), as achieving this value would likely result in a reduction of FFP biomass. Overabundant FFP in aquatic systems can be an important symptom of eutrophication (Croft and Chow-Fraswer 2007), and a better understanding of its response to various key drivers should help to inform future management actions.

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