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Environmental factors controlling phytoplankton dynamics in a large floodplain river with emphasis on cyanobacteria

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Abstract

Harmful algal blooms are occurring in large river ecosystems and at the mouth of large rivers with increasing frequency. In lentic systems, the chemical and physical conditions that promote harmful algal blooms are somewhat predictable but tracking prevalence and conditions that promote harmful algal blooms in lotic systems is much more difficult. We captured two of the most extreme discharge years within the last 20 years occurring in the Upper Mississippi River, allowing a natural experiment that evaluated how major shifts in discharge drive environmental variation and associated shifts in phytoplankton. Statistical models describing significant environmental covariates for phytoplankton assemblages and specific taxa were developed and used to identify management-relevant numeric breakpoints at which environmental variables may promote the growth of specific phytoplankton and/or cyanobacteria. Our analyses supported that potentially toxin-producing cyanobacteria dominate under high phosphorus concentration, low nitrogen concentration, low nitrogen-to-phosphorus ratio, low turbulence, low flushing, adequate light and warm temperatures. Cyanobacteria dominated in 2009 when low discharge and low flushing likely led to optimal growth environments for *Dolichospermum*, *Aphanizomenon* and *Microcystis*. Rarely will a single factor lead to the dominance, but multiple positive factors working in concert can lead to cyanobacteria proliferation in large rivers. Certain isolated backwaters with high phosphorus, low nitrogen, warm water temperatures and low potential for flushing could benefit from increased connection to channel inputs to reduce cyanobacterial dominance. Numerous examples of this type of habitat currently exist in the Upper Mississippi River and could benefit from reconnection to channel habitats.

KEYWORDS

algal blooms, connectivity, cyanobacteria, eutrophication, phosphorus, phytoplankton, Upper Mississippi River

1 | INTRODUCTION

Toxic cyanobacteria blooms are on the rise globally and are occurring in large river ecosystems and at the mouth of large rivers with increasing frequency (Huisman et al., 2018; O'Neil, Davis, Burford, & Gobler, 2012; Paerl & Otten, 2013). Algal blooms cause decreased clarity, reduced macrophytes, oxygen depletion, fish kills and the production of cyanotoxins (Paerl & Otten, 2013). The production of cyanotoxins can result in illness and/or death of exposed pets and occasionally humans. Cyanotoxins are especially concerning when

blooms occur in drinking water supply locations (Cheung, Liang, & Lee, 2013). High phosphorous concentration, low nitrogen concentration, low nitrogen-to-phosphorous (N:P) ratio, low turbulence, low flushing, adequate light and warm water temperature conditions are all known to promote cyanobacterial blooms (Baker & Baker, 1979; Dodds & Smith, 2016; Elliot, 2012; Schindler, Carpenter, Chapra, Hecky, & Orihel, 2016; Wehr & Descy, 1998). In lentic systems, the chemical and physical conditions that promote harmful algal blooms are somewhat predictable but tracking prevalence and conditions that promote harmful algal blooms in lotic systems is much more difficult.

The heterogeneity of habitats and continuous movement of water in large river ecosystems make understanding ecological dynamics especially challenging. Expansive lateral connectivity between high-velocity main channel waters and lower-velocity off-channel areas requires application of lentic and lotic models that must then be integrated based on levels of connectivity and water exchange. Annual variation in discharge and water level further complicates understanding in large river ecosystems. Shifting water levels, seasonally and annually, change residence times, connectivity, and riparian/littoral interactions (K. K. Baker & Baker, 1981; Remmal, Hudon, Hamilton, Rondeau, & Gagnon, 2017). Light and temperature also change seasonally, and timing of water level shifts is highly correlated with seasonal changes in discharge relating to thaw and overland runoff. Discharge is directly related to water residence time, water depth and dilution rates (Wehr & Descy, 1998). The multidimensional and ever-changing physical environment in large rivers makes predicting biological dynamics difficult.

Phytoplankton dynamics are tightly tied to variable physical conditions in both lentic and lotic systems. Early work in lotic systems focused heavily on light and residence time as factors driving phytoplankton dynamics (Baker & Baker, 1981). High water velocity washes out phytoplankton, especially cyanobacteria (Baker & Baker, 1979, 1981; Huisman et al., 2004). Differential sinking rates of taxa depend on buoyancy (Baker & Baker, 1981) and the shape of cells (Reynolds & Irish, 1997). Different sinking rates interact with water velocity and turbulence (Bouma-Gregson, Power, & Bormans, 2017; Reynolds, 1994) to drive highly variable taxa-specific light environments for species living in riverine environments (Remmal et al., 2017; Reynolds & Descy, 1996). Seasonal shifts in overland run-off change sediment load and directly impact light availability for benthic and water column primary producers. Overland run-off, suspended solids, discharge, water-velocity, residence times and dilution are all directly linked for many river systems, and each physical factor impacts the types and volume of primary producers present in river habitats.

More recent work acknowledges the role of nutrients in driving lotic phytoplankton dynamics (Bussi et al., 2016; O'Neil et al., 2012). The relationship between nutrients and phytoplankton in lentic environments is well established (Carpenter, Booth, Kucharik, & Lathrop, 2015; Smith, 1986). The heavy application of nitrogen-rich fertilizers to agricultural fields, increasing human waste and increasing atmospheric deposition have resulted in rapid increases in nitrogen (N) concentrations in North America (Galloway & Cowling, 2002; Smith & Schindler, 2009). In some systems, where N-fixation fails to meet phytoplankton requirements, reductions in N loading can bring about a reversal in eutrophication. However, in most cases, phosphorus (P) loading is generally viewed as the predominant driver of increased phytoplankton production, especially for cyanobacteria (O'Neil et al., 2012; Schindler, 1978; Schindler et al., 2016). High nutrient waters are often associated with elevated biovolume of potentially toxin-producing cyanobacteria (Paerl & Otten, 2013).

The ratio of N–P (N:P) plays a role in driving phytoplankton dynamics if either nutrient becomes limiting (Dodds & Smith, 2016; Dolman, Mischke, & Wiedner, 2016; Dolman & Wiedner, 2015). Heavy P loading relative to N loading results in low N:P, which can favour cyanobacteria dominance, especially for N_2-fixing genera (Downing, Watson, & McCauley, 2001; Smith, 1983). Profound seasonal shifts in N and P are frequently observed in the Upper Mississippi River (UMR) and have been related to shifts in biological productivity, ranging from chlorophyll a shifts to transitions in free-floating plant dominance (Giblin et al., 2014; Houser, Bierman, Burdis, & Soeken-Gittinger, 2010).

Prior studies of phytoplankton on the UMR have demonstrated a 40-fold increase in phytoplankton biomass following impoundment in the 1930s (Baker & Baker, 1981). The large increase in phytoplankton biomass post-impoundment is concerning in the UMR since a substantial proportion of UMR phytoplankton is comprised of potentially toxin-producing cyanobacteria (Decker, Wehr, Houser, & Richardson, 2015; Paerl & Otten, 2013). Our data include the growing season of phytoplankton and environmental monitoring data collected in 2009 and 2011 across replicated backwater and main channel sites in Pool 8 of the UMR. We captured two of the most extreme flow years within the last 20 years, allowing a natural experiment that evaluates how major shifts in discharge drive environmental variation and shifts in phytoplankton between extreme hydrologic conditions in the UMR. Analyses include the quantification of potentially toxin-producing cyanobacteria genera to test how these taxa are impacted by environmental variation.

2 | MATERIALS AND METHODS

2.1 | Study site

The UMR consists of a series of navigation pools extending from Minneapolis, MN to the confluence of the Ohio River at Cairo, IL, USA. The 27 navigation dams within this area 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 (Anfinson, 2003; Sparks, 1995). Navigation pools are unlike reservoirs, in that, they remain mostly riverine in nature. More detailed descriptions of these contrasting aquatic areas can be found in Strauss et al. (2004).

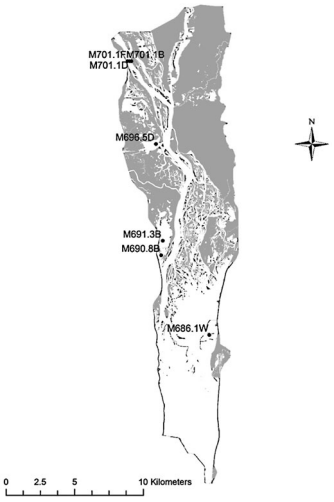


FIGURE 1 Location of study sites within Navigation Pool 8 of the Upper Mississippi River

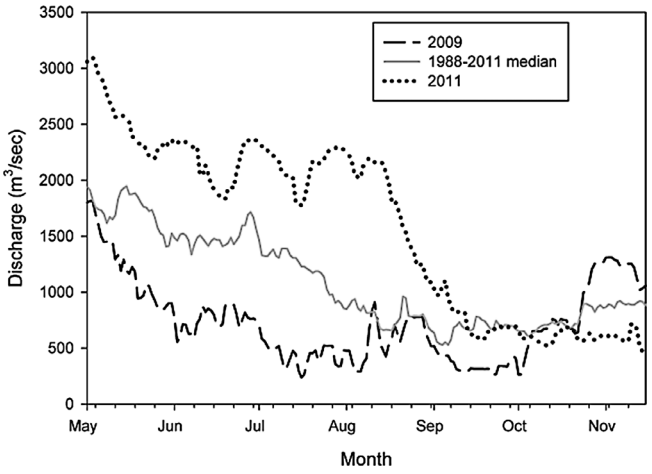


FIGURE 2 Discharge ($m^3\ s^{-1}$) at Lock and Dam 8 during 2009 and 2011 by Julian date. The long-term median (1988–2011) is denoted with a solid line

Collections took place in Navigation Pool 8 of the UMR (Figure 1), a 39 km long, ~90 km^2 stretch of river located between Lock and Dam 7 (Dresbach, MN, USA) and Lock and Dam 8 (Genoa, WI, USA). Pool 8 is a highly heterogeneous stretch of large river habitat where the area of water in backwaters is 19.4 km^2 compared with 12.6 km^2 flowing through the main channel. Pool 8 also includes 36.9 km^2 of open-water, impounded the area upstream of the downstream dam and 13.2 km^2 of the side channel habitat (Strauss et al., 2004; Wilcox, 1993). The main channel is >3 m deep and is characterized by water velocities of 0.20–1 m s^{-1}. Side channels are lotic but exhibit depth and water velocity that are generally less than the main channel. Backwaters typically exhibit very low water velocity (often below detection) and are connected to main or side channel habitats at mean river stage. The average water residence time in Pool 8 is 1.7 days (Wasley, 2000), but this number is influenced by the changing volume of water moving through the main channel—water residence time in backwaters may range from days to months.

2.2 | Sampling and data collection

Our data were collected as part of the Long-Term Resource Monitoring (LTRM) program on the UMR, which has been observing water quality, aquatic plant and fish communities since 1993. Part of the federally mandated Upper Mississippi River Restoration (UMRR) program, LTRM conducts annual assessments using both fixed and spatially stratified randomized sampling designs (Soballe & Fischer, 2004). This study utilized fixed-site sampling data from seven sites within Navigational Pool 8 of the UMR. Three sites (M701.1B, M701.1D, M701.1F) were main channel sites sampled as a lateral transect near Dresbach, MN (Figure 1). There is a lateral gradient among these three sites based on differences in water moving in and out of backwater complexes upstream. Site M701.1B is the most different among the three sites as it is ~2 km downstream of the outlet of a large backwater complex (Lake Onalaska). The four remaining sites sampled (M686.1W, M690.8B, M691.3B and M696.5D) were backwater sites representing a wide range of connection to channel inputs (Figure 1). The composite of these seven sites represents a substantial range of the limnological variability within the UMR and collectively represent a realistic view of water quality condition and, therefore, phytoplankton assemblage, in Pool 8 of the UMR. Analysing all seven sites together was an a priori decision designed to represent a realistic range of limnological conditions across varied levels of connectivity to the main channel in Pool 8. Discharge in 2009 was consistently less than the long-term median, whereas 2011 discharge was consistently greater than the long-term median (Figure 2). The combination of high discharge and low discharge years resulted in a dataset representative of a robust range of environmental conditions.

2.3 | Water quality and discharge

Water samples were collected by inverting a 2-L amber bottle at a depth of 0.20 m at each site to assess water column total suspended solids (SS), total nitrogen (TN) and total phosphorus (TP) concentrations. SS was determined gravimetrically following standard methods (Greenberg, Clesceri, & Eaton, 1992). TN and TP samples were preserved in the field with concentrated H_2SO_4, transported on ice, and refrigerated until analysis. TN and TP were determined colorimetrically using standard methods (Greenberg et al., 1992). Measurements of water depth (m) and water velocity (m sec^{-1}; 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). Further details regarding LTRM field methods can be found in Soballe and Fischer (2004). Discharge data were collected by the U.S. Corps of Engineers at Lock and Dam 8 (LD8) at Genoa, WI and measured in $m^3\ s^{-1}$.

TABLE 1 Wilcoxon signed-rank sum test results indicating the *Z-statistic and p value* for environmental covariates between paired dates in late 2009 and late 2011 in Pool 8 of the Upper Mississippi River

Variable	Late 2009			Early 2011			Late 2011			Late 2009 vs. Late 2011	
	25th	Median	75th	25th	Median	75th	25th	Median	75th	Z	*p*
Water temperature (°C)	18.4	22	23.8	11.5	16.7	21	20	24	26	*−3.86*	*<.001*
TP: Total phosphorus (mg L^{-1})	0.073	0.162	0.186	0.064	0.08	0.092	0.086	0.131	0.158	2	*.046*
TN: Total nitrogen (mg L^{-1})	0.73	0.96	1.34	2.27	2.62	3.07	0.98	1.49	2.91	*−4.65*	*<.001*
N:P: Nitrogen to phosphorous by mass	5.6	7.5	13.3	29.8	35.9	39.9	9.2	12.4	33.9	*−3.1*	*.002*
SS: Total suspended solids (mg L^{-1})	1.5	3.1	6.2	9.3	11.2	15.2	1.9	7.1	11.7	*−4.05*	*<.001*
Water depth (m)	0.87	1.59	5.20	1.62	2.36	6.55	1.59	2.04	5.60	*−4.55*	*<.001*
Water velocity (m s^{-1})	0.000	0.020	0.140	0	0.03	0.86	0.000	0.000	0.460	*−2.1*	*.036*
Discharge at lock and dam 8 (m^3 s^{-1})	360	651	706	2,141	2,456	2,908	821	2033	2,186	*−4.72*	*<.001*

Note: The early 2011 data, from May 4 to June 13, are presented for demonstrative purposes. The 25th percentile, median and 75th percentile are also presented for each timeframe.

2.4 | Phytoplankton

Phytoplankton samples were collected in conjunction with water chemistry samples, preserved with Lugol's solution and stored in amber bottles at room temperature until enumeration was performed. Samples were collected during 2009 (n = 30; from 1 July to 7 October) and 2011 (n = 84; from 4 May to 7 November). Phytoplankton enumeration was performed during August of 2014. Phytoplankton enumeration was performed by BSA Environmental Services (Beachwood, OH, USA). Phytoplankton slides were prepared using a standard membrane filtration technique (McNabb, 1960). This technique preserved the cell structure and provided good resolution for both the 2009 and 2011 samples, allowing them to be examined at high magnifications. Samples were thoroughly mixed as a part of the filtering process to ensure that the organisms were evenly distributed. A Leica DMLB compound microscope (100×, 200×, 400×, 630×, 1000×) was used for enumerating filtered phytoplankton samples. The magnification used depended upon the size of dominant taxa and presence of particulates. The goal was to count at multiple magnifications such that enumeration and identification of taxa, which vary over several orders of magnitude in size, was achieved. If a sample was dominated by cells or natural units below 10–20 μm, or when cells were fragile and difficult to identify, most of the counting was completed at 630×. The abundance of common taxa was estimated by random field counts. At least 400 units (colonies, filaments, unicells) were enumerated and identified to the lowest possible taxonomic level for each sample. In accordance with Lund, Kipling, and LeCren (1958), counting 400 natural units provided accuracy within 90% confidence limits. In addition, an entire strip of the filter was counted at high magnification (usually 630×) along with half of the filter at a lower magnification (usually 400×) to further ensure complete species reporting. Cyanobacteria were assigned to trait-separated functional groups as defined by Reynolds, Huszar, Kruk, Naselli-Flores, and Melo (2002).

Cell biovolumes of all identified phytoplankton taxa were quantified on a per liter basis. Biovolumes (in μm^3 L^{-1}) were estimated using formulae for solid geometric shapes that most closely match the cell shape (Hillebrand, Dürselen, Kirschtel, Pollingher, & Zohary, 1999). Biovolume calculations were based on measurements of 10 organisms per taxon for each sample where possible.

For taxa with substantial size variation (such as diatoms), size classes were designated arbitrarily to determine average cell size (biovolume). For each taxon, 25 cells were measured from each size class, assuming that sufficient numbers were available. Mean biovolumes within each size class were used to calculate the total biovolume contributed by the taxon to its representative sample (Burkholder & Wetzel, 1989).

2.5 | Statistical analyses

Differences among water chemistry, discharge and site physical characteristics between the two sampling years were analysed using a

Wilcoxon signed-rank test using the coin package in R (Hothorn, Hornik, Van De Wiel, & Zeileis, 2008). Samples were paired from June 29 to October 7 for both years utilizing samples that occurred within 5 days of each other during the different sampling years.

Phytoplankton biovolumes were converted to relative volume based on sampling date and collection location. Canonical correspondence analysis (CCA) was conducted using the matrix of phytoplankton taxa relative volume tested against a suite of environmental variables (water depth, water temperature, water velocity, total suspended solids [SS], total phosphorous [TP], total nitrogen [TN] and nitrogen-to-phosphorous ratio by mass [N:P]). The output of CCA provides quantification of the variability within the plankton community and breaks out how much of that variation can be explained by the specified environmental factors. Rather than present CCA ordinations for each date, we used the breakdown of variation from the CCA analyses to represent how environmental factors impact phytoplankton community assemblage throughout the 2009 and 2011 sampling periods.

Critical environmental thresholds predictive of phytoplankton biovolume were modelled using a regression tree analysis (rpart, R Core Development Team, 2011). The tree was built by selecting the single variable that best split the data into two groups. This

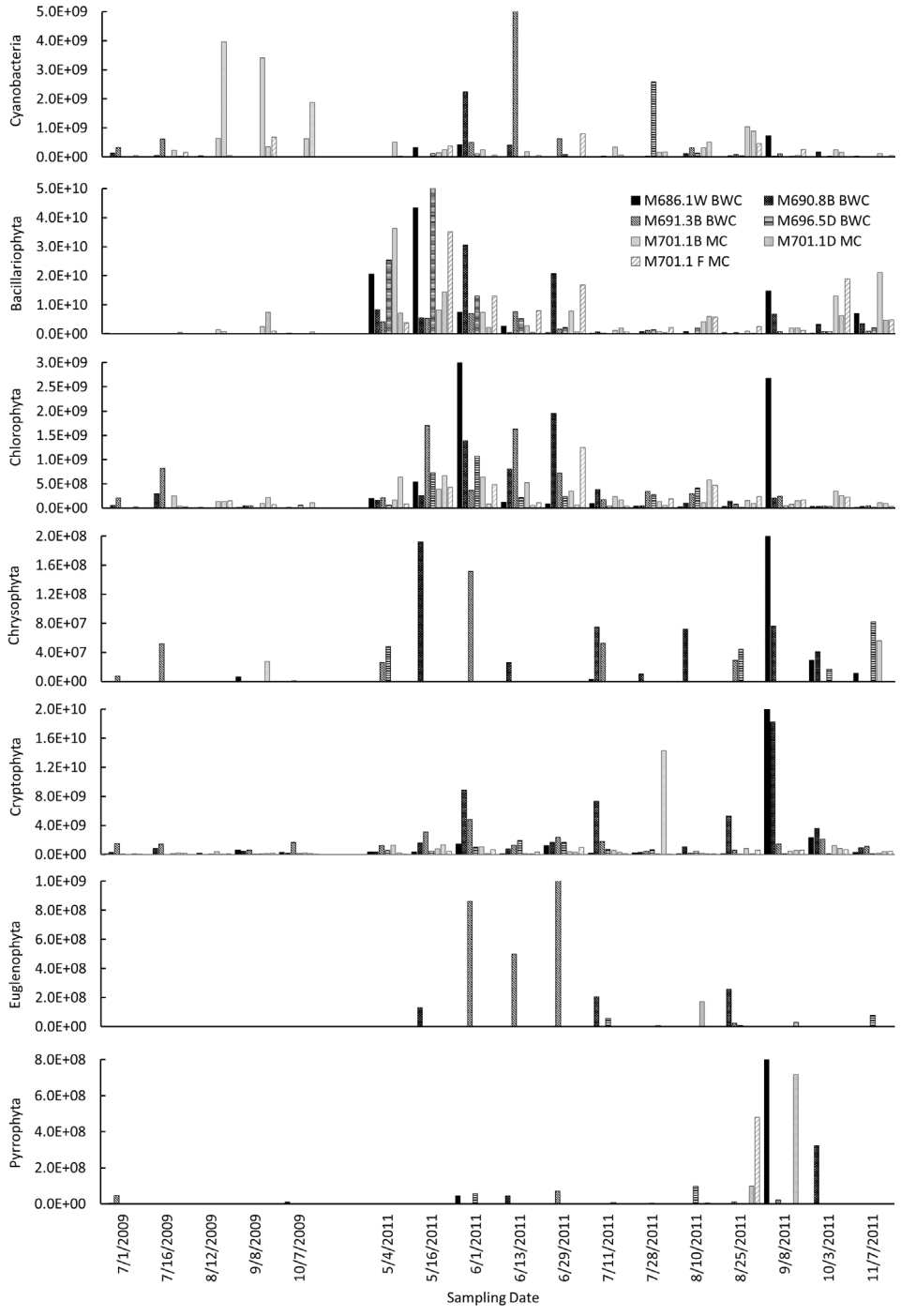
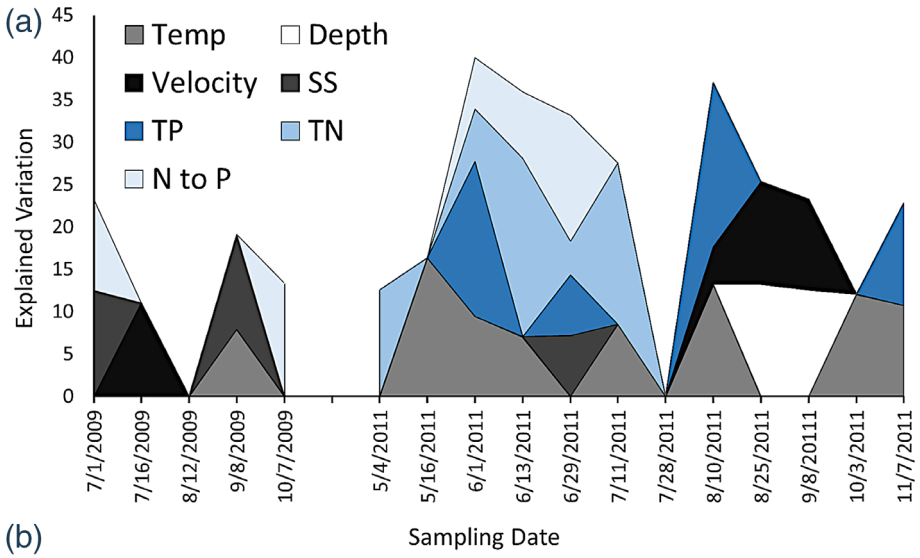


FIGURE 3 Phytoplankton biovolume (in $\mu m^3\ L^{-1}$) for "phyla" across dates in 2009 and 2011 from backwater and main channel habitats of the Upper Mississippi River. Backwater (BWC) sites are outlined in black colour and main channel (MC) sites are shaded in grey colour



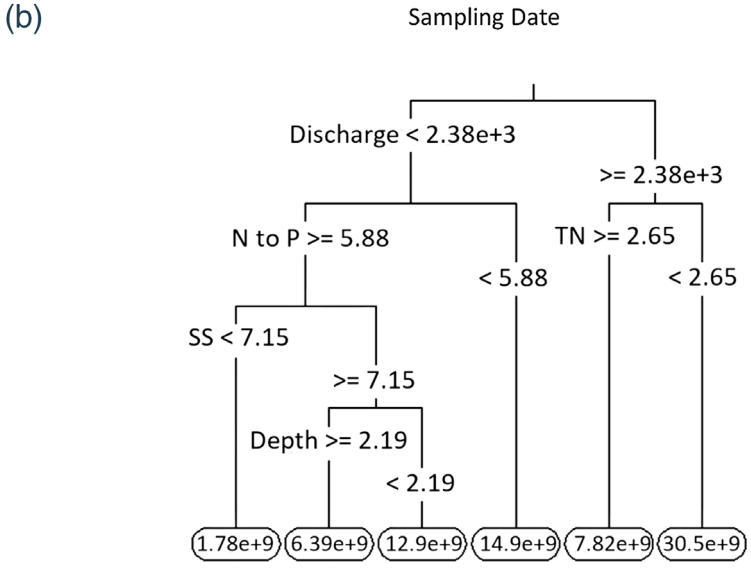


FIGURE 4 Environmental predictors of phytoplankton taxa abundances in 2009 and 2011. (a) Values represent the amount of variation in phytoplankton assemblage explained by each environmental factor as determined using PCA variance partitioning. (b) Regression tree model of predictors across all dates and all habitats. Predicted total phytoplankton biovolume for each branch of the tree is in the lower ovals. The numeric breakpoint for each parameter defining a branch is presented on each split

process was then performed on each sub-group until no further improvement can be made (Therneau, Atkinson, Ripley, & Ripley, 2018). For each model, phytoplankton, toxin-producing cyanobacteria or a specific taxa biovolume served as the response variable tested using uniform environmental covariates (discharge, water depth, water temperature, water velocity, SS, TP, TN and N:P). TP was significantly correlated with soluble reactive phosphorus (SRP; r^2 = .866, p < .05), and TN was significantly correlated with dissolved inorganic nitrogen (DIN; r^2 = .948, p < .05). TP and TN were used for analysis due to being highly correlated with dissolved nutrients and commonly used among the river management community relative to dissolved nutrients. The regression models provide relevant numeric breakpoints for each explanatory environmental covariate.

3 | RESULTS

River discharge differed significantly between 2009 and 2011 (Table 1, Figure 2). With these extreme differences in discharge, physical and chemical environmental parameters also differed significantly between 2009 and 2011. Values for SS, TN, N:P, water temperature, water velocity and water depth were significantly higher in 2011 than in 2009, while TP was significantly lower in 2011 than in 2009 (Table 1). Growth limiting dissolved nutrient concentrations were observed during both years using thresholds suggested by Maberly et al. (2002; <100 μg L^{-1} for DIN and <10 μg L^{-1} for SRP). In 2009 and 2011, respectively, 33 and 18% of samples were below the DIN threshold, while 7 and 32% of samples were below the threshold for SRP.

Biovolume of primary producers differed between 2009 and 2011 (Figure 3). In 2009, volume and taxa richness (# of phyla at each site) were lower, and the river was dominated by cyanobacteria, which reached highest biovolumes in the main channel sites (Figure 3). Overall phytoplankton biovolume and taxonomic richness were much higher in 2011, especially in backwater habitats. Community composition shifts occurred throughout the summer months of 2011. Diatoms (Bacillariophyta) and green algae (Chlorophyta) dominated the early and mid-summer water column while Cryptophyta and Pyrrophyta were more abundant in late summer (Figure 3). It is possible that these

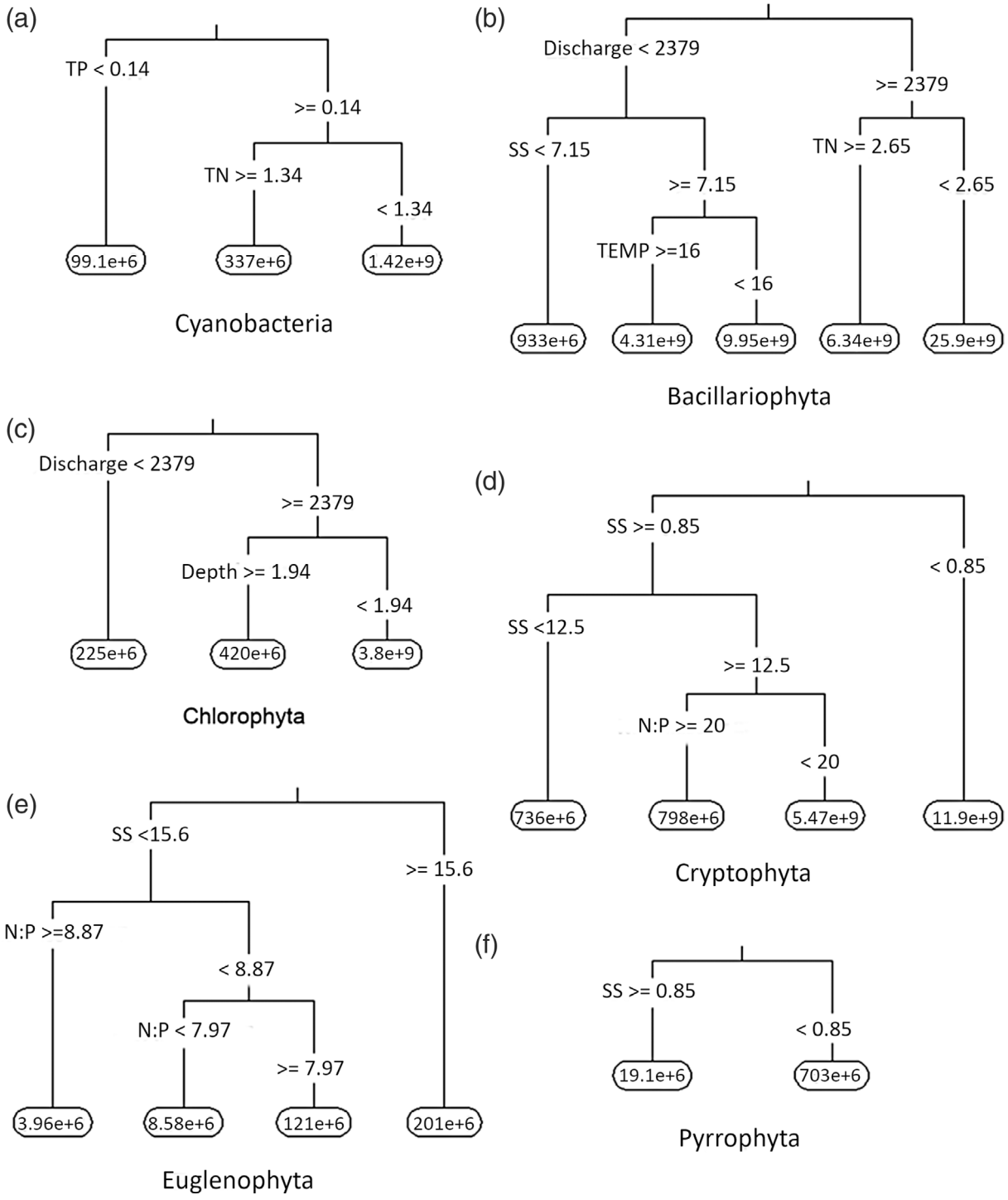


FIGURE 5 Regression tree models predicting specific phytoplankton "phyla" biovolume (in $\mu m^3 L^{-1}$) using uniform environmental covariates: (a) Cyanobacteria, (b) Bacillariophyta, (c) Chlorophyta, (d) Cryptophyta, (e) Euglenophyta, (f) Pyrrophyta. Predicted biovolume for each branch of the tree is in the lower ovals. The numeric breakpoint for each parameter defining a branch is presented on each split

early season taxa were not captured in 2009 since sampling in 2009 did not begin until early July.

Low numbers of phytoplankton and limited taxa representation resulted in low overall variation of primary producers in 2009 (Figure 3). Variation in the 2009 phytoplankton assemblage was mostly explained by differences in physical traits like SS and water velocity (Figure 4a). Higher variation in phytoplankton assemblage was observed in 2011. During the high-water period in early summer 2011 (5/4–7/11), nutrients (TP, TN and N:P) explained the majority of variation in phytoplankton assemblage. In late summer 2011

TABLE 2 Phytoplankton taxa related to explanatory environmental covariates based on general regression tree models

	Higher discharge	Warmer water temperature	Higher TP	Higher TN
General	Higher total biovolume	Lower Bacillariophyta biovolume	Higher cyanobacteria biovolume	Lower total biovolume
Regression	Higher Bacillariophyta biovolume	Higher *Microcystis* biovolume	Higher potentially toxic cyanobacteria biovolume	Lower Bacillariophyta biovolume
Tree	Higher Chlorophyta biovolume		Higher *Dolichospermum* biovolume	Lower cyanobacteria biovolume
Trends	Lower *Aphanizomenon* biovolume		Higher *Aphanizomenon* biovolume	Lower potentially toxic cyanobacteria biovolume
			Higher *Microcystis* biovolume	

	Higher N:P ratio	Higher SS*	Greater water depth	Higher water velocity
General	Lower total biovolume	Higher total biovolume	Lower total biovolume	Lower potentially toxic cyanobacteria biovolume
Regression	Lower Cryptophyta biovolume	Higher Bacillariophyta biovolume	Lower Chlorophyta biovolume	
Tree	Higher Euglenophyta biovolume	Higher *Dolichospermum* biovolume	Lower *Dolichospermum* biovolume	
Trends		Higher *Pseudanabaena* biovolume	Lower *Pseudanabaena* biovolume	
		Higher *Planktothrix* biovolume		

*Higher within study sites; maximum SS = 21.9 mg L^{-1}.

(8/10–11/7), as high waters receded, physical parameters (temperature, water depth and water velocity) explained more variation in phytoplankton assemblage (Figure 4a).

Regression tree models of environmental covariates support that discharge explains phytoplankton differences between 2009 and 2011 and between early and late 2011 (Figure 4b). TN and N:P ratio were also drivers of total phytoplankton biovolume. Low levels of nitrogen (<2.65 mg L^{-1}) and low N:P ratio (<5.88) in 2009 allowed for nitrogen-fixing cyanobacteria to outcompete eukaryotic algae. It follows that TP and TN are the only significant environmental factors explaining the variation in cyanobacteria volume (Figure 5a). High discharge (>2,379 m^3 s^{-1}), low TN (<2.65 mg L^{-1}), high SS (>7.15 mg L^{-1}) and cooler water temperature (<16°C) tended to result in higher Bacillariophyta biovolume (Table 2, Figure 5b). Chlorophyta biovolume was highest at high discharge and reduced water depth (Table 2, Figure 5c). Cryptophyta, Euglenophyta and Pyrrophyta volumes were explained by the variation in SS and N:P ratio (Table 2, Figure 5d–f).

Cyanobacteria biovolume was further analysed to evaluate environmental drivers of potentially toxin-producing genera. Differences among the five potentially toxin-producing cyanobacteria genera (*Dolichospermum*-previously *Anabaena*, *Aphanizomenon*, *Microcystis*, *Pseudanabaena* and *Planktothrix*) were observed between the 2 years (Table S1). *Microcystis*, *Aphanizomenon* and *Dolichospermum* were dominant during the low discharge conditions of 2009 (Figure 6). *Pseudanabaena* and *Planktothrix* were more dominant during higher discharge periods of 2011 (Figure 6). Variation in cyanobacteria volume was best explained by suspended solids and nutrient ratios in 2009, while more variation in genera was explained by physical factors (temperature, water depth, SS and water velocity) throughout 2011 (Figure 7a).

The regression tree for the five potentially toxin-producing cyanobacteria genera supported that TP and TN concentrations were the major explanatory factors (Figure 7b, Table 2). The highest predicted biovolume for potentially toxin-producing cyanobacteria was under high TP conditions (≥0.14 mg L^{-1}), in conjunction with low TN (<1.34 mg L^{-1}). High *Dolichospermum* biovolume occurred with higher SS, shallow water depth (<0.815 m) and high TP (>0.185 mg L^{-1}; Table 2, Figure 8a). *Aphanizomenon* was the highest at high TP (≥0.186 mg L^{-1}) and lowest with lower TP and higher discharge conditions (>467 m^3 s^{-1} Table 2, Figure 8b). The highest *Microcystis* biovolume was predicted under high TP conditions, while the lowest predicted biovolume was with low TP (<0.14 mg L^{-1}; Table 2, Figure 8c). Water temperature also played a role, with sites greater than 24.3°C showing high *Microcystis* biovolume. *Pseudanabaena* and *Planktothrix* exhibited similar patterns in relation to environmental factors. *Pseudanabaena* biovolume was highest under shallow conditions (<1.19 m) with higher SS (≥2.2 mg L^{-1}; Table 2, Figure 8d). *Planktothrix* biovolume was highest at elevated SS (≥15.8 mg L^{-1}) and lowest at reduced SS (<8.45 mg L^{-1}; Table 2, Figure 8e).

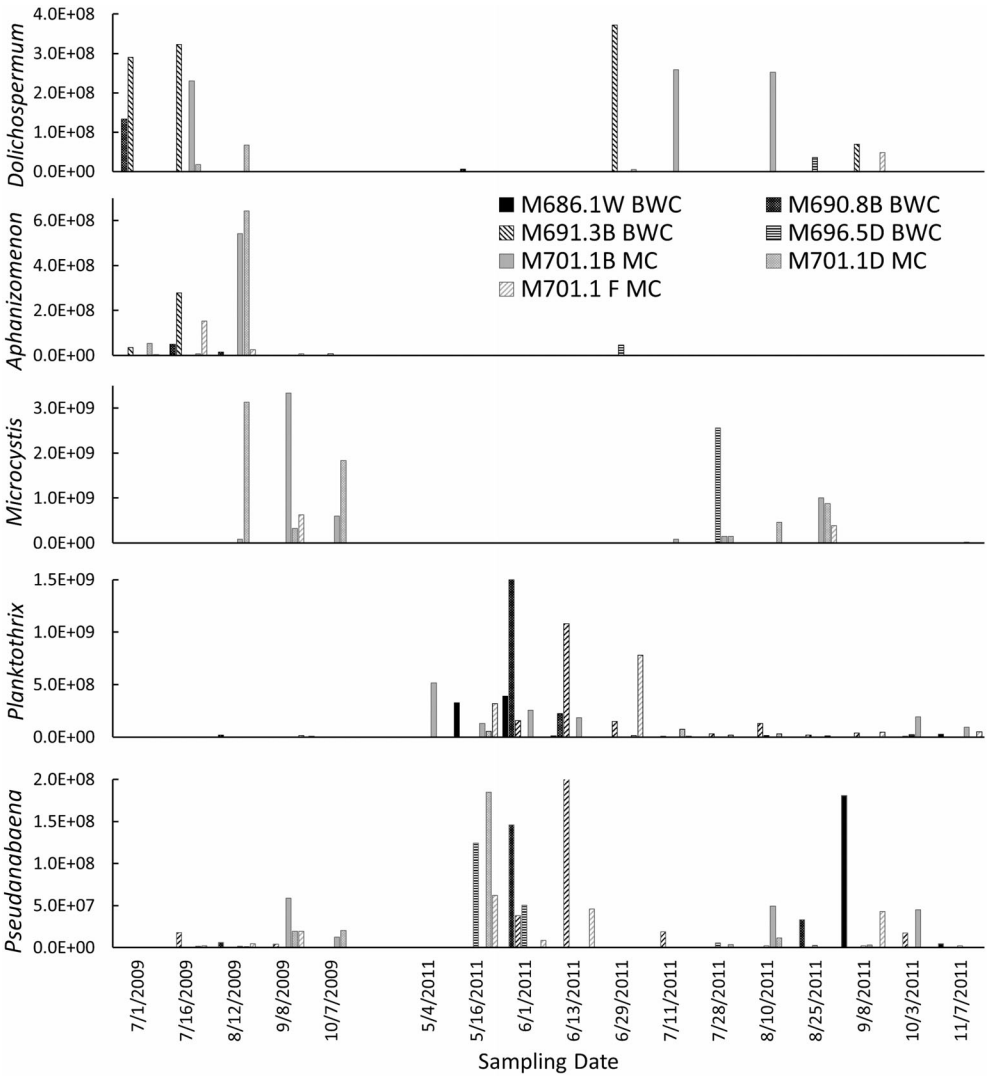


FIGURE 6 Cyanobacteria biovolume (in $\mu m^3\ L^{-1}$) for genera across dates in 2009 and 2011 from backwater and main channel habitats of the Upper Mississippi River. Backwater (BWC) sites are outlined in black colour and main channel (MC) sites are shaded in grey colour

Large differences in the physical and chemical environments between 2009 and 2011 resulted in profound differences in the phytoplankton community assemblage. Trait-separated functional groups, S1 and R (as described by Reynolds et al., 2002), which are tolerant of low light, were dominant during high discharge in 2011 (Table 3). Conversely, functional groups, SN, H1, LM and M, which are tolerant of high light, low TN, and sensitive to flushing, poor light and low TP, were dominant during low discharge in 2009 (Table 3).

4 | DISCUSSION

Cyanobacteria dominated in 2009 when water level and discharge were much lower. This finding supports the previous work that low discharge, low water velocity and reduced water depth correspond to increased water clarity and higher water temperature to promote harmful algal blooms (Descy, 1993). Both the variance partitioning and regression show that physical characteristics are prominent drivers of the cyanobacteria community composition in both 2009 and 2011. Nutrient ratios explain less variation, overall, but help explain the 2009 succession of cyanobacterial species. In 2009, the increase in *Dolichospermum* and *Aphanizomenon* during early summer low discharge, low nitrogen and high phosphorus conditions is partially attributable to their sensitivity to flushing and tolerance of low dissolved inorganic nitrogen (Paerl & Otten, 2013; Reynolds et al., 2002). *Dolichospermum* achieved its greatest dominance at site M691.3B, the most isolated backwater site, as dissolved inorganic nitrogen was below 100 $\mu g\ L^{-1}$ in July of 2009. *Aphanizomenon* production was also stimulated in the backwaters during July of 2009 and may have seeded the main channel blooms that were observed in August of 2009.

Our results closely follow detailed evaluations of optimal cyanobacteria temperatures, with *Dolichospermum* and *Aphanizomenon* dominance at intermediate water temperature and *Microcystis* dominance at higher temperatures (Dokulil & Teubner, 2000; Paerl & Otten, 2016; Robarts & Zohary, 1987). The late summer 2009 dominance of *Microcystis* (a non-N fixer) under low discharge is likely explained by its tolerance of high light, affinity for elevated TP, and its

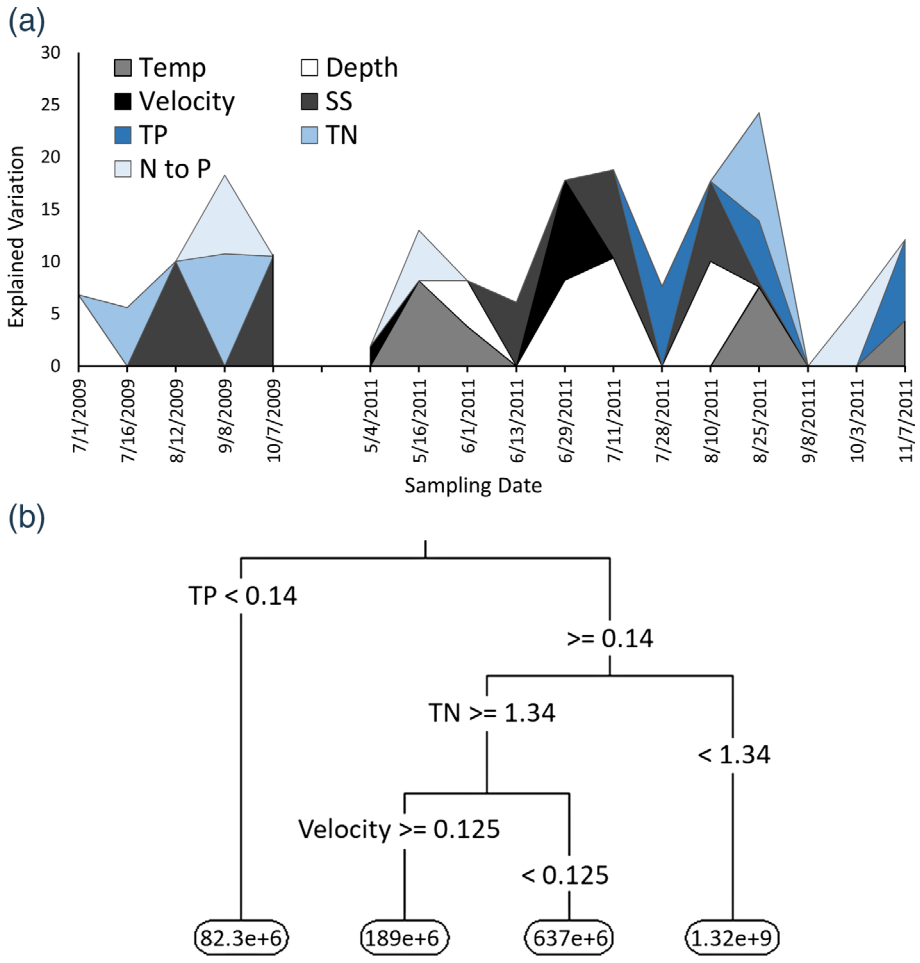


FIGURE 7 Environmental predictors of cyanobacteria genera abundances across 2009 and 2011. (a) Values represent the amount of variation in cyanobacteria assemblage explained by each environmental factor as determined using PCA variance partitioning. (b) Regression tree model. Predicted total toxin-producing cyanobacteria genera biovolume for each branch of the tree is in the lower ovals

ability to optimize position in the water column under conditions of minimal turbulence (Ha, Cho, Kim, & Joo, 1999; Ibelings, Mur, & Walsby, 1991). *Microcystis* also achieves dominance at elevated water temperatures (Dziallas & Grossart, 2011).

In the main channel, a late summer transition to *Microcystis* was observed in 2009. This trend of main channel dominance of *Microcystis* was not observed in the high discharge conditions of 2011. The difference was likely related to low growth rates typical of *Microcystis*, making it intolerant of short residence time (Lehman et al., 2017; Mitrovic, Hardwick, & Dorani, 2011). *Aphanizomenon* is also susceptible to shorter residence and was less abundant in 2011 (Paerl et al., 2016). Differing levels of turbulent flow have also been reported to determine the presence of cyanobacteria in river systems (Williamson, Kobayashi, Outhet, & Bowling, 2018). Elevated *Aphanizomenon* and *Microcystis* biovolume have previously been reported under low discharge conditions worldwide, including the UMR (De Leon & Yunes, 2001; Descy, 1993; Ha et al., 1999; Mitrovic et al., 2011; Williamson et al., 2018). During the low discharge of 2009, it is likely that backwater areas, upstream of the main channel transect, served as a seed source to the main channel (Sommer, Harrell, & Swift, 2008). *Aphanizomenon* is large and buoyant, resulting in competitive advantage under low discharge conditions (Köhler, 1994). *Microcystis* can optimize position in the water column under lower turbulence conditions to harvest light (Huisman et al., 2004; Ibelings et al., 1991). *Microcystis* and *Aphanizomenon*, which are known to be intolerant of low light, were also dominant under low SS conditions (De Leon & Yunes, 2001; Ha et al., 1999; Reynolds et al., 2002). Conversely, the dominance of *Planktothrix* and *Pseudanabaena* during low light is likely linked to their ability to tolerate the higher turbidity (Reynolds et al., 2002).

The general paradigm of increasing cyanobacterial dominance, especially potentially toxin-producing genera, under high phosphorus concentration, low nitrogen concentration, low N:P ratio, low turbulence, low flushing, adequate light and warm temperatures, was supported in our analysis of the UMR (Paerl & Otten, 2013). Rarely will a single factor lead to the dominance, but multiple positive factors working in concert can lead to cyanobacteria proliferation. The principal action to reduce cyanobacteria biovolume is the reduction of nutrients, with phosphorus reductions being of foremost importance. Certain isolated backwaters, with high phosphorus, low nitrogen, warm water temperatures and low potential for flushing, could benefit from increased connection to channel inputs to reduce cyanobacterial dominance (Paerl, Hall, & Calandrino, 2011). Numerous examples of

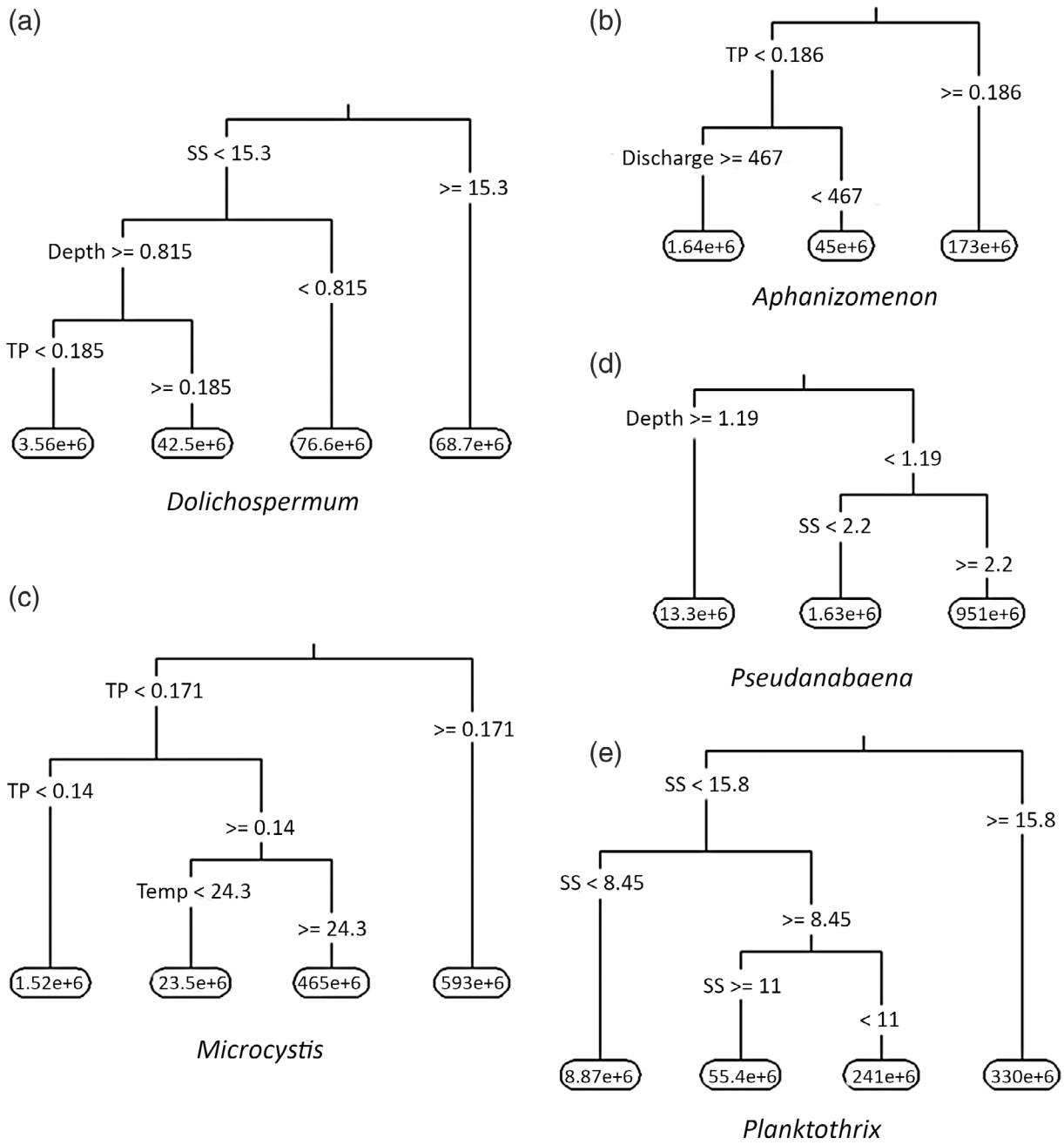


FIGURE 8 Regression tree models predicting specific cyanobacteria genera biovolume (in $\mu m^3\ L^{-1}$) using uniform environmental covariates: (a) *Dolichospermum*, (b) *Aphanizomenon*, (c) *Microcystis*, (d) *Pseudanabaena*, (e) *Planktothrix*. Predicted biovolume for each branch of the tree is in the lower ovals. The numeric breakpoint for each parameter defining a branch is presented on each split

this type of habitat currently exist in the UMR and could benefit from reconnection to channel habitats.

Climate change scenarios and the increased dominance of cyanobacteria at water temperatures >25°C would predict increased dominance of cyanobacteria into the future (Paerl & Huisman, 2008; Wells et al., 2020). Extreme precipitation events are likely to increase in the future, resulting in increased nutrient loading (Carpenter et al., 2015). What is currently unclear is how the interplay between increased flushing and increased nutrient loading due to increased precipitation will play out (Kreiling & Houser, 2016). Additional future predictions involve increased hypoxia and increased internal loading of phosphorus related to backwater hypoxia at the sediment interface (Paerl et al., 2011). While reducing external nutrient input is the most direct method to reduce cyanobacterial dominance, mitigation measures to alter connectivity to the main channel will improve conditions if backwater residence time is decreased sufficiently (Paerl et al., 2016). Backwater sediment removal to reduce internal nutrient loading within the UMR will also have high potential to lessen cyanobacterial dominance related to expected climate change.

TABLE 3 Trait-separated functional groups of cyanobacteria described by Reynolds et al. (2002)

Codon	Habitat	Tolerances	Sensitivities	Year dominant
S1	Turbid mixed layers	Highly light-deficient conditions	Flushing	2011
SN	Warm mixed layers, P rich, low N	Light, nitrogen-deficient conditions	Flushing	2009
H1	Eutrophic, but with low N (N-fixers)	Low nitrogen, low carbon	Mixing, poor light, low phosphorus	2009
LM	Summer epilimnia in eutrophic lakes	Very low C	Mixing, poor stratification, light	2009
M	Mixed layers of small eutrophic, low latitude lakes	High insolation (light)	Flushing, low total light	2009
R	Metalimnia of stratified lakes	Low light, strong segregation	Instability	2011

Note: Preferred habitat type, tolerances, sensitivities and year dominant for each functional group are presented.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author, SMG, upon reasonable request.

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SUPPORTING INFORMATION

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