

Seston, Light, Nutrients and Chlorophyll in the Lower Missouri River, 1994-1998

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ABSTRACT

We collected data for five years from the lower Missouri River including discharge ($819-10032 \text{ m}^3 \text{ s}^{-1}$), mean depth (2.7-9.3 m), underwater irradiance ($0.1 - 3.7 \text{ Ein m}^{-2} \text{ d}^{-1}$), suspended solids ($19-2340 \text{ mg L}^{-1}$), total phosphorus ($131-1810 \text{ } \mu\text{g L}^{-1}$), total nitrogen ($0.9-4.2 \text{ mg L}^{-1}$), nitrate-N ($380-3050 \text{ } \mu\text{g L}^{-1}$), silica ($8.2-16.8 \text{ mg L}^{-1}$) and chlorophyll ($4.5-107 \text{ } \mu\text{g L}^{-1}$). Suspended solids, phosphorus and light attenuation varied directly with discharge. Nitrate, ammonium-N, silica and chlorophyll were strongly seasonal. Chlorophyll was temperature dependent exhibiting winter minima ($<8 \text{ } \mu\text{g L}^{-1}$) and spring and fall maxima ($>40 \text{ } \mu\text{g L}^{-1}$). In the growing season, chlorophyll co-varied with light and varied inversely with silica and dissolved P. Poor light conditions (mixed depth:photic depth >10) and rapid flow rates ($\approx 150 \text{ km d}^{-1}$) suggest that *in situ* production of algae is less important than flux of biomass from upstream. Chlorophyll flux and pheophytin increased with discharge indicating contributions of benthic or terrestrial inputs. About a fourth of the particulate organic nitrogen transported by the river may be autochthonous. Algal uptake may reduce silica flux by $>22\%$.

INTRODUCTION

The Missouri River drains about 17% of the continental U.S. and contributes about 13% of the Mississippi River discharge to the Gulf of Mexico. The modern river is a highly engineered system with flow controlled by seven mainstem dams and more than 70 dams on major tributaries (Hesse and Mestl 1993). The lower 1183 km of the river is channelized for navigation and bounded by flood-control levees (Slizeski et al. 1982) that result in greater water depths and faster flow than in the pre-development era (Galat et al. 1996).

Transport of sediment, nutrients and other materials by the river is increasingly important because of their possible contribution to seasonal hypoxia in the Gulf of Mexico (Rabalais et al. 1996, 1999). Material transport, nutrient concentrations and primary productivity are also important components of the Missouri River ecosystem. The river is home to about 260 species of fish including several listed as rare or endangered (Galat et al. 1996).

Following the record flood of 1993, research on the Missouri River ecosystem has intensified (Galat et al. 1998). As part of that work, we collected a five-year series of water quality data including measurements of suspended material, nutrients, and chlorophyll. Together with data on

river bed morphology, these data provide insight into the seasonality of material transport by the river and factors controlling primary productivity by riverine algae.

METHODS AND MATERIALS

One or more sites on the lower Missouri River, 283-398 river kilometers (RK) upstream from the Missouri-Mississippi river confluence, were sampled year-around between March 1994 and March 1999, usually biweekly. Sampling was conducted as part of a floodplain habitat evaluation (Knowlton and Jones 1997, Galat et al. 1998) and water quality monitoring of a constructed wetland (Eagle Bluffs Conservation Area). Surface water samples (2 L) were collected and water temperature measured (YSI Model 54 Temperature/Oxygen Meter) from shore or by boat, always in locations with strong current.

Water samples were analyzed for chlorophyll (CHL - Knowlton 1984, Sartory and Grobbelaar 1984), total phosphorus (TP - Prepas and Rigler 1982), total nitrogen (TN - Crumpton et al. 1992), suspended solids (American Public Health Association 1985), nephelometric turbidity (Hach Model 18900 turbidimeter), and absorbance (ABS) at 440 nm (Kirk 1983). Suspended solids were measured gravimetrically from the residue retained by glass-fiber filters (Whatman 934-AH). Total, volatile (550°C), and non-volatile fractions of suspended solids (TSS, VSS, and NVSS, respectively) were determined. Filtrates from suspended solids determinations were analyzed for dissolved TP and dissolved TN (dTP, dTN), dissolved inorganic N (DIN), including nitrate-nitrite-N ($\text{NO}_3\text{-N}$ - American Public Health Association 1985) and ammonium-N ($\text{NH}_4\text{-N}$ - Stainton et al. 1977), silica (American Public Health Association 1985), ABS, and nephelometric turbidity. All analyses except ABS and turbidity were performed in duplicate. Except where noted in the text, chlorophyll data are presented uncorrected for degradation products.

Daily river stage (m) and discharge ($\text{m}^3 \text{s}^{-1}$) estimates for the Missouri River at Boonville, Missouri were obtained from the U.S. Geological Survey. A bathymetric map and stage-discharge model developed by the U.S. Army Corps of Engineers (1998) for a ≈ 6 km reach of the Missouri River near Rocheport, Missouri (Rocheport Bend, RK 297-303) was used to estimate the relation between surface area, mean water column depth (Z), and river stage (S) at the Boonville gauge 13 km upstream. For discharge (Q) $< 6400 \text{ m}^3 \text{ s}^{-1}$ the relation for mean depth was:

$$Z = 2.08 + 0.39 \cdot S + 0.057 \cdot S^2$$

Approximate incident irradiance was estimated from monthly means of daily pyrhelimeter records ($n=5072$) from several recording sites in Missouri during 1992-1995 (P. Guinan, Missouri Climate Center, University of Missouri, Columbia, MO U.S.A. 65211, personal communication). Monthly means ranged from 5.7 MJ d^{-1} for December to 21.3 MJ d^{-1} for July. Pyrhelimeter measurements were converted to photosynthetically active radiation (PAR) assuming $1 \text{ MJ total shortwave irradiance} = 2.05 \text{ Ein PAR}$ (Stefan et al. 1983). Attenuation of PAR (k in

m^{-1}) was estimated from ABS ($-\log_{10}$ transmittance in a 1 cm light path) at 440 nm from a regression model based on absorbance and *in situ* light attenuation (LiCor quantum meter) in a turbid Missouri reservoir (Knowlton and Jones 1995):

$$\log_{10}(k) = 1.22 + 0.70 \cdot \log_{10}(\text{ABS})$$

Mean water column irradiance (*Irrad* – Ein $m^{-2} d^{-1}$) was calculated according to Riley (1957):

$$Irrad = PAR \cdot (1 - e^{-(k \cdot Z)}) \cdot (k \cdot Z)^{-1}$$

RESULTS

During the study, discharge ranged from 819 to 10032 $m^3 s^{-1}$ (Table 1, Fig. 1a) with a corresponding range of 8.7 m in the river surface elevation at Boonville, Missouri. Average discharge during the study (2515 $m^3 s^{-1}$) was 129% of average discharge during 1970-1992. Minimum annual flow (819-1222 $m^3 s^{-1}$) occurred in winter (December-January). Flood stage at Boonville ($\approx 4400 m^3 s^{-1}$) was exceeded 21 times during the study (Fig. 1a) for periods of 1-54 days (total = 165 of 1857 days). Mean water column depth (Fig. 1b) based on the morphology of the reach at Rocheport Bend averaged 4.7 m (Table 1) during periods when discharge was within the range of mean depth calibration ($< 6400 m^3 s^{-1}$). During periods of higher discharge in May-June 1995 (25 days) and 1996 (8 days) and for shorter periods in 1997 and 1998 (3-6 days each), mean depth was not estimated. Over-bank flow during these floods probably reduced mean depth relative to what could be extrapolated from the Rocheport Bend morphology data.

Table 1. Means and ranges of water quality data – March 1994 through March 1999.

	n	Mean	Minimum	Maximum
Q ($m^3 s^{-1}$)	1866	2519	819	10032
Z (m)	1816	4.7	2.7	9.3
k (m^{-1})	132	9.2	1.9	39.0
<i>Irrad</i> (Ein $m^{-2} d^{-1}$)	125	1.0	0.1	3.7
TSS ($mg L^{-1}$)	121	341	19	2340
VSS ($mg L^{-1}$)	121	28	2	180
TP ($\mu g L^{-1}$)	132	407	131	1810
dTP ($\mu g L^{-1}$)	132	119	64	209
TN ($mg L^{-1}$)	132	2.2	0.9	4.2
dTN ($mg L^{-1}$)	132	1.8	0.6	3.8
NO ₃ -N ($\mu g L^{-1}$)	132	1310	380	3050
NH ₄ -N ($\mu g L^{-1}$)	131	53	<20	290
SiO ₂ ($mg L^{-1}$)	119	12.1	8.2	16.8
CHL ($\mu g L^{-1}$)	132	23.6	4.5	107
Si:NO ₃ -N (atomic ratio)	119	2.4	1.1	5.8

Light attenuation increased predictably with discharge ($\log_{10}(k) = -2.84 + 1.10 \cdot \log_{10}(Q)$, $n=118$, $r^2=0.61$, $MSE=0.035$) and ranged from 1.9 to 37.6 m^{-1} (mean=9.3 m^{-1} , Table 1). Photic depth (1% incident light) averaged 0.78 m and ranged from 0.12 to 2.4 m. For the Rocheport Bend reach, an average of 7.5% of the river bottom (range 0.02-38.0%) was within the photic zone. Mixed depth:photic depth ratios averaged 10.2 (range 1.2 to 55), and mean water column irradiance (Table 1) averaged 1.0 $E_{in} m^{-2} d^{-1}$ ($\approx 4\%$ of incident light). *Irrad* usually peaked in winter due to the minimal water depths and reduced turbidity associated with seasonally low flow (Fig. 1c), but these measurements take no account of light attenuation by ice flows which occasionally cover much of the river in midwinter. Our information on the extent and duration of ice cover is insufficient to judge the magnitude of this bias.

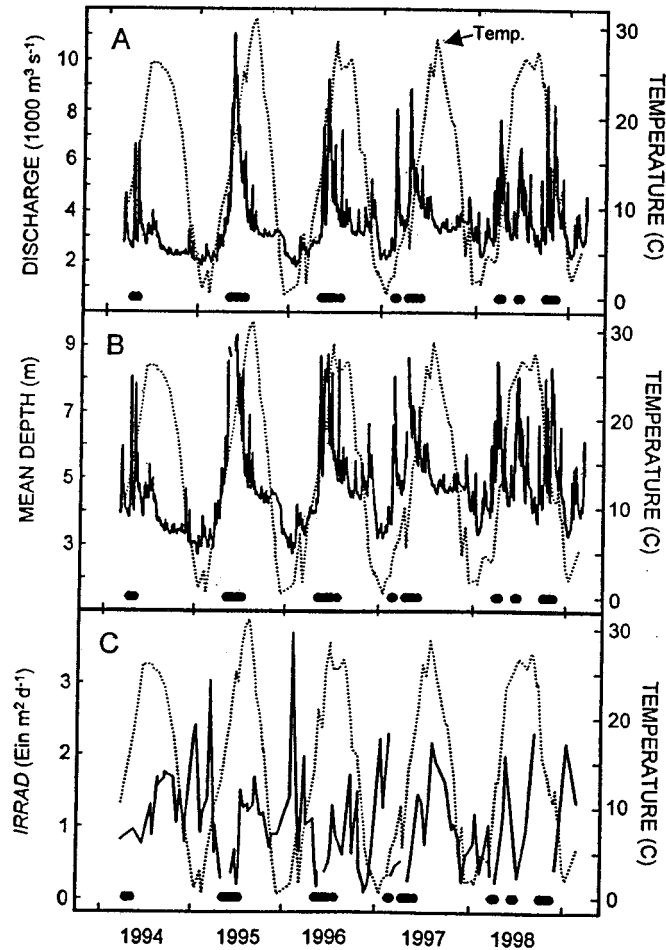


Figure 1. Time series of Missouri River temperature, discharge, mean water column depth and mean water column irradiance - 1994-1998. Circles above the X-axis mark days when the river was above flood stage at Boonville, Missouri.

Light attenuation, TSS, and TP were highly intercorrelated ($r > 0.95$) and exhibited nearly identical patterns of temporal variation. As shown by TP data in Fig. 2a, values peaked during floods and were minimal during winter low-flow periods. Concentrations were highly variable during floods, but using \log_{10} transformation to standardize variance, regression models show discharge to account, respectively, for 57% and 66% of the temporal variation in TP and TSS (Table 2). Due to the correlation of concentrations with flow, discharge accounted for $>80\%$ of the temporal variation in TP and TSS flux (flux = concentration \cdot discharge - Table 2).

Averages of 62% of TP and 90% of light attenuation were removed by filtration (Whatman 934 AH filters). Filterable ("dissolved") TP (Fig. 2a) also peaked during floods, probably because of particulate P in fine sestonic material not retained by the filters. Nephelometric turbidity in filtered water (TSS filtrates) averaged 11% of total turbidity (range = 5-32%) and was also correlated with discharge ($r=0.81$, $n=132$, $p<0.0001$, \log_{10} transformed data). The larger fraction of particulate P (TP minus dTP) closely covaried with the corresponding fraction of turbidity (total minus filterable, $r=0.97$, $n=132$, $p>0.0001$). In the range of turbidity exhibited by the filterable fraction (1-132 NTU), this relation had a slope of $1.7 \mu\text{g L}^{-1}$ P per NTU. Assuming this same relation for the filterable fractions of TP and turbidity, an average of 20% of filterable TP was

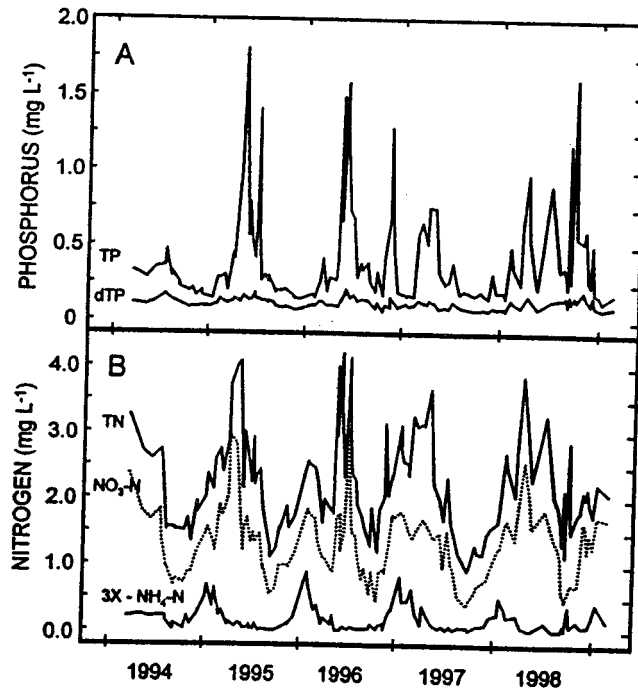


Figure 2. Time series of total and dissolved phosphorus, total nitrogen, nitrate-nitrite-N and ammonium-N in the Missouri River 1994-1998. Ammonia-N data are plotted at three times their actual values.

particulate (range -7 to 98%). Corrected for this fraction, dissolved TP was negatively correlated with discharge ($r = -0.34$, $n = 132$, $p < 0.0001$) but this trend may be an artifact of the turbidity correction (i.e., over-correction for high-discharge, high turbidity observations).

Total N was only weakly dependent on flow ($r^2 = 0.08$ – Table 2) and, unlike TP, often peaked during low-flow periods (Fig. 2b). Nitrate-N was usually the largest component of TN (mean=59%, range= 22-81%) followed by filterable (“dissolved”) organic N (DON = dTN-DIN) which averaged 20% of TN (range 6-38%). DON was positively related to discharge ($r^2 = 0.16$ – Table 2). DON also covaried with filterable turbidity ($r = 0.54$, $n = 131$, \log_{10} transformed data) and probably included some fine particulate N. The relation of $\text{NO}_3\text{-N}$ to discharge was not significant and $\text{NH}_4\text{-N}$ varied inversely with flow (Table 2). Ammonium-N concentrations averaged only $53 \mu\text{g L}^{-1}$ during the study (Table 1) and was never more than 11% of TN. Both $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ were distinctly seasonal with $\text{NH}_4\text{-N}$ always peaking in mid to late-winter during periods of low flow. $\text{NO}_3\text{-N}$ exhibited a late-summer decline and annual minimum in September-October in each year of the study (Fig. 2b). Discharge accounted for 57-78% of the temporal variation in flux of $\text{NO}_3\text{-N}$, TN and DON but had no significant relation to flux of $\text{NH}_4\text{-N}$ (Table 2).

Chlorophyll concentration uncorrected for degradation products (CHL) averaged $23.6 \mu\text{g L}^{-1}$ with a range of 4.5 to $107 \mu\text{g L}^{-1}$ (Table 1). CHL was predictably seasonal. Annual minima (4.5 to $8.0 \mu\text{g L}^{-1}$, Fig. 3a) occurred in winter each year (December-February) at water temperatures $< 4^\circ$. CHL increased with temperature in spring and declined with temperature in autumn (Fig. 3a). $\text{CHL} > 30 \mu\text{g L}^{-1}$ ($n = 30$) was only observed at temperatures $> 10^\circ$. In regression, temperature accounted for 48% of temporal variation in CHL (Table 2).

Annual maximum CHL (42 - $107 \mu\text{g L}^{-1}$) usually occurred in fall (September-October), but dual (vernal and autumnal) maxima were observed every year except in early 1994 when less frequent sampling (monthly) may have missed the peak (Fig. 3a). Vernal and autumnal CHL peaks co-occurred with peaks in underwater light (Fig. 3b). At water temperatures greater $> 10^\circ$, CHL covaried with *Irrad* ($r = 0.69$, $n = 80$, $p < 0.0001$). At winter temperatures ($< 4^\circ$), however, CHL was usually low ($n = 21$, mean= 8.0 , range 4.5 - $12.5 \mu\text{g L}^{-1}$) despite the high *Irrad* that often accompanied low discharge during the winter period (Fig. 3b). Because of the seasonality of the response to light, addition of *Irrad* to the CHL-temperature regression (Table 2) yielded no significant improvement in explained variation.

Low irradiance and high turbidity during floods were usually accompanied by lower CHL than observed at lesser flow rates in the same range of temperature. At temperatures $> 10^\circ$, CHL was negatively correlated with discharge ($r = -0.52$, $n = 86$, $p < 0.0001$). Nonetheless, flux of CHL was positively related to discharge (Table 2), even if data from cooler, low flow periods were excluded (for temperatures $> 10^\circ$, $r = 0.40$, $n = 86$, $p < 0.0001$, \log_{10} transformed data). Relatively high CHL was measured during floods despite high turbidity. CHL in samples with TSS $> 500 \text{ mg L}^{-1}$ ($n = 23$) ranged from 6.8 to $28.5 \mu\text{g L}^{-1}$ (mean = $18.0 \mu\text{g L}^{-1}$). The fact

Table 2. Selected bivariate regressions for material concentrations (mg L⁻¹), material flux (g s⁻¹), Q (m³ s⁻¹) and temperature (°C). All variables except temperature were transformed to base-10 logs. Comparable regressions without significant (p<0.05) slopes (NO₃-N, CHL, and NH₄-N_{flux} versus Q, SiO_{2flux} versus CHL) are not shown.

Dependent	Independent	n	Slope	Intercept	r ²	MSE
TSS	Q	121	1.82	-3.85	0.664	0.074
TSS _{flux}	Q	121	2.82	-3.85	0.826	0.074
TP	Q	132	0.95	-0.71	0.569	0.032
TP _{flux}	Q	132	1.95	-0.71	0.847	0.032
TN	Q	132	0.20	-0.34	0.084	0.020
TN _{flux}	Q	132	1.20	-0.34	0.771	0.020
DON	Q	131	0.31	-1.45	0.163	0.022
DON _{flux}	Q	131	1.31	-1.45	0.775	0.022
NO ₃ -N _{flux}	Q	132	1.02	0.03	0.571	0.036
NH ₄ -N	Q	123	-0.80	1.21	0.123	0.020
CHL	Temperature	132	0.021	-2.03	0.478	0.041
CHL _{flux}	Q	132	1.17	-2.29	0.446	0.078
SiO ₂	Q	119	-0.16	1.62	0.195	0.005
SiO ₂	CHL	119	-0.18	0.77	0.410	0.003
SiO _{2flux}	Q	119	0.84	1.62	0.865	0.005

that CHL flux increased with discharge despite unfavorable growth conditions at high flow, suggests recruitment of algae (or pigmented detritus) from benthic or terrestrial sources.

Pheophytin was routinely measured after June 1996 and averaged 43% of total chlorophyll (chlorophyll + pheophytin) in samples with TSS>500 mg L⁻¹ (n=11, range 31-58%). In samples with TSS<500 mg L⁻¹, pheophytin averaged 30% of total chlorophyll (n=42, range 10-48%). Pheophytin content did not notably decline during spring and fall CHL maxima, averaging 28% of total chlorophyll when CHL >40µg L⁻¹ (n=7, range 22-26%). Pheophytin content was lowest in winter, averaging 20% of total chlorophyll at water temperatures <4° (n=11, range 10-40%). In comparison, pheophytin in samples collected contemporaneously from nearby floodplain oxbows and scour ponds not connected to the river (Knowlton and Jones 1997, University of Missouri unpublished data) averaged 20% overall (n=188, range 0-64%) with means of 19% at CHL>40 µg L⁻¹ (n=83, range 0-40%) and 15% at temperatures <4° (n=29, range 0-35%).

Organic seston (VSS) averaged 28 mg L⁻¹ during the study (Table 1) and was usually a minor component of total seston (mean = 9% of TSS, range 4-15%). Algal biomass, in turn, was a minor component of VSS. Assuming a CHL content of 2% of ash-free dry weight (Reynolds 1984), algal biomass during the study averaged 1.2 mg L⁻¹. Seston in the river

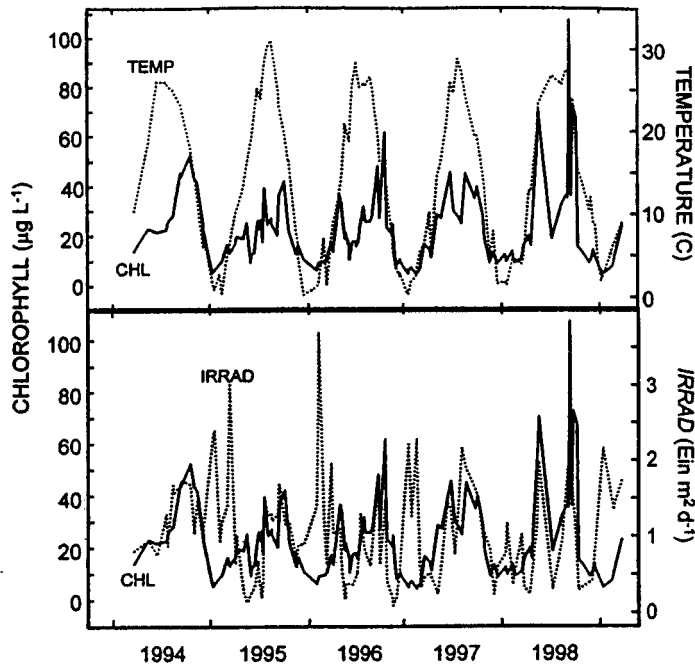


Figure 3. Time series of chlorophyll, temperature and mean water column irradiance.

contained relatively low amounts of N and P. Particulate TN (TN-dTN) and TP (TP-dTP), respectively averaged only 0.24% and 0.11% of TSS. In contrast, algal biomass typically contains 6% N and 1% P (Hecky and Kilham 1988). Based on these percentages, algal biomass estimated from CHL averaged only 8% of particulate P and 4% of TN, but averaged 23% of particulate N. Thus algal biomass contributed little to total N flux, but may have been an important component of the particulate organic N (PON) fueling the river food web.

We estimate an annual range of algal biomass averaging $\approx 3 \text{ mg L}^{-1}$ of which about 0.2 mg L^{-1} was PON. In comparison, the annual range of DIN averaged 2.1 mg L^{-1} (Fig. 2b). Thus fluctuations in phytoplankton biomass were probably too small to contribute greatly to temporal variation in DIN. Minimal $\text{NO}_3\text{-N}$ in early autumn (Fig. 2b) always coincided with relatively high CHL (Fig. 3), but a direct causal link between the two events seems unlikely.

Algal growth, probably did help regulate SiO_2 . Silica (as SiO_2) averaged 12.1 mg L^{-1} during the study (Table 1) and was negatively correlated with flow (Table 2). Silica varied over time in nearly direct opposition to CHL, as would be expected if algal uptake was reducing ambient silica concentration (Fig. 4a). Peaks in CHL were accompanied by declines in silica on a nearly point by point basis throughout the study period. In regression, variation in CHL accounted for 41% of the temporal variability in SiO_2 (Table 2). Nonetheless, because silica varied by only a factor of two during the study (Table 1), flux of SiO_2 was mostly a function of discharge ($r^2 = 0.87$). In a multiple regression:

$\log_{10}(\text{SiO}_2 \text{ flux}) = 0.87 \cdot \log_{10}(Q) - 0.16 \cdot \log_{10}(\text{CHL}) + 1.23$
 (n=119, $r^2=0.92$, MSE=0.003, units as in Table 2), variation in CHL accounted for only 6% of the variation in silica flux not due to flow. From this relationship, we estimated that total SiO₂ flux for the days with silica and CHL measurements (n=119) would have declined by about 27% (from 30650 g s⁻¹ to 22500 g s⁻¹) if CHL was constant at the maximum concentration observed during the study (107 μg L⁻¹). Holding CHL at the observed minimum (4.5 μg L⁻¹) would yield a 22% increase in silica flux.

Algal growth may also have influenced dissolved P concentrations. In time series plots, several of the larger CHL peaks were accompanied by sharp declines in dTP (Fig. 4b), suggesting reduction of dissolved P by algal uptake. And at temperatures >10°, dTP was negatively correlated with CHL ($r = -0.43$, $p < 0.0001$, $n = 86$). But given that dTP and CHL were related in opposite directions to flow, this trend may be an artifact of multiple co-linearity.

Atomic ratios of silicon (in silica) to nitrogen (in nitrate-nitrite) averaged 2.4 during the study (Table 1) and varied inversely with NO₃-N ($r = -0.83$). Silicon:nitrogen was minimal during winter/spring NO₃-N peaks but never reached the 1:1 level at which silicon and nitrogen are in stoichiometric balance for diatom growth (Rabalais et al. 1996).

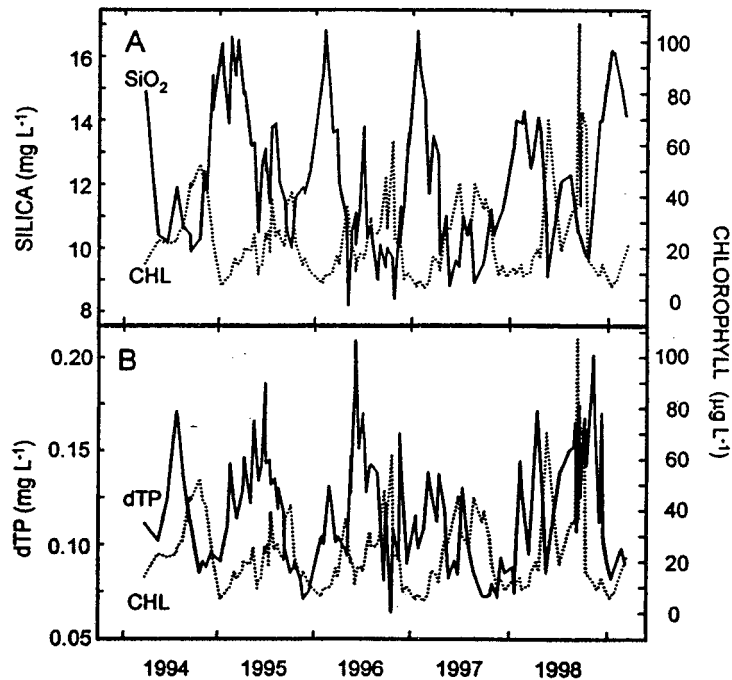


Figure 4. Time series of chlorophyll, silica and dissolved total phosphorus.

DISCUSSION

Inputs of N and P from anthropogenic sources in the Mississippi River catchment has greatly increased nutrient loading to the Gulf of Mexico in the past 50 years (Turner and Rabalais 1991) and has shifted stoichiometric ratios of N, P and Si to favor greater frequency of P and Si limitation (Rabalais et al. 1996). Nutrients from the Mississippi River fuel primary production in Louisiana coastal waters that contribute to seasonal hypoxia in bottom waters in the northern Gulf of Mexico (Rabalais et al. 1999). Concern about "Gulf Hypoxia" has led to intensified research on sources and sinks of riverine nutrients in the Mississippi and its tributaries culminating in extensive reports assembled by "Task Groups" commissioned by the United States White House Committee on Environment and Natural Resources (e.g. Rabalais et al. 1999, Goolsby et al. 1999, Brezonik et al. 1999). Among the conclusions offered by these groups is that too little is known about processing of nutrients in large rivers. Such systems may act simply as conduits, conservatively transporting all the materials they receive, or may significantly reduce biologically available forms of N, P and Si.

Our CHL data suggest a considerable amount of autochthonous production in the Missouri River. Flux of CHL (CHL · discharge) averaged $\approx 5400 \text{ kg d}^{-1}$ which represents about 270,000 kg d^{-1} of algal biomass (assuming 2% CHL content) or 100 million kg yr^{-1} . Presumably, riverine phytoplankton contribute to this total, but benthic and external sources may influence these results. Thus factors related to primary production deserve close scrutiny.

Nutrient concentrations suggest that phytoplankton and benthic algae in our study area were never nutrient-limited. Concentrations of DIN, and SiO_2 were always much higher than those likely to saturate algal uptake and growth ($\approx 1\text{-}14 \mu\text{g L}^{-1}$ DIN, $<0.5 \text{ mg L}^{-1}$ SiO_2 - Reynolds 1984). We did not measure inorganic P, but filterable P was never below $64 \mu\text{g L}^{-1}$ (Table 1), whereas only $3 \mu\text{g L}^{-1}$ of orthophosphate will usually satisfy algal growth requirements (Reynolds 1992).

If nutrients are saturating then light and temperature will largely control algal growth rates (Bannister 1974). In our study area, photosynthesis was usually, if not always, light-limited. During the growing season (May-September) an average of only 4% of the river bottom was in the photic zone and mean water column irradiance averaged only $1 \text{ Ein m}^{-2} \text{ d}^{-1}$ or $<3\%$ of incident PAR. These averages correspond to a mean mixed depth over 10 times the photic depth. In other nutrient-saturated system, production and respiration typically balance at photic:mixed depth ratios closer to 1:1 (Wofsy 1983). Light required for net algal growth varies widely among species (Kirk 1983), but it is likely that circulating phytoplankton in the lower Missouri River are rarely, if ever, light-saturated and may usually have P/R ratios <1 . The persistence of elevated pheophytin in our samples, even during CHL peaks, supports the idea that our study site may tend toward heterotrophy.

Based solely on light conditions, it seems unlikely our study area has a net positive carbon balance. But the CHL and other materials measured in the study originate far upstream where conditions may be more favorable. For the Rocheport Bend reach, flow rate (discharge divided by mean channel cross section) averaged 1.7 m s^{-1} for periods with mean depth estimates (discharge $<6400 \text{ m}^3 \text{ s}^{-1}$). With travel rates averaging $\approx 150 \text{ km d}^{-1}$, CHL we measured may include outputs from upstream reservoirs which produce over half the flow reaching our study area. Hesse et al. (1982) concluded that most of the phytoplankton found in the Missouri River in eastern Nebraska was derived from the plankton of mainstem impoundments 250–450 km upstream from their study sites. Our samples came from sites $>500 \text{ km}$ farther downstream where reservoir releases represent a smaller proportion of discharge, but with travel times of only about one week, limnoplankton from impoundments could be important in CHL dynamics in the lower Missouri River. Likewise algae produced in tributary streams could be important (Van Nieuwenhuysse and Jones 1996). We lack comparative morphological or light data, but it is likely that light conditions in Missouri River tributaries are far less severe than in the mainstem which is dominated by a deep navigation channel (Slizeski et al. 1982).

During the growing season (temperature $>10^\circ$), CHL in our study area declined during floods; nonetheless, CHL flux increased significantly with discharge. This finding, together with the elevated pheophytin we observed during floods, suggests that benthic or terrestrial sources of pigment may be important. Sestonic CHL in streams sometimes increases during floods due to entrainment of benthic algae (Perkins and Jones 1994). Also, soils in agricultural fields may contain $>500 \text{ kg ha}^{-1}$ of algal biomass (Lund 1967), mostly concentrated near the surface where entrainment with runoff is likely. Terrestrial plant detritus could also be present eroded soils. Thus several sources of pigment in addition to autochthonously produced phytoplankton may have contributed to CHL dynamics in the river.

Regarding nutrient removal or transformation in the river, it seems unlikely that autochthonous processes have major effects on net flux of bioavailable N or P, at least in the river mainstem. Algal growth may remove some inorganic N and P, but in the absence of net removal processes (denitrification, loss through the food chain, permanent sediment deposition, etc.) N and P so sequestered are likely to be remineralized downstream. Net removal of N and P is probably more important in reservoirs and lower-order tributaries than in the river mainstem (Smith et al. 1997).

Silica concentrations do seem dependent on algal growth as is probably typical of many streams (Wall et al. 1998). We have no means of estimating total SiO_2 removal that occurs upstream of our study site. But from the regression model relating SiO_2 flux to CHL and discharge, average silica flux would increase 22% if minimal CHL ($4.5 \mu\text{g L}^{-1}$) was maintained in the river. Assuming that some SiO_2 uptake takes place even at minimal CHL, total in-stream removal of silica may be substantially higher.

The environmental group, American Rivers, has ranked the Missouri River as the second most "endangered" rivers in the U.S. (American Rivers 1999), and controversy over management of the river's flow regime and floodplain is intense. Proposals for "restoring" the river (Galat et al. 1996) include measures that would decrease flow rates and average water depth (e.g. expansion of floodplain wetlands, creation of side channels, etc.). These changes could improve light conditions and stimulate algal growth thus increasing depletion of silica and might also increase N removal through denitrification. Knowlton and Jones (1997) showed that floodplain lakes connected to the Missouri River produce algal blooms and rapidly exhaust NO₃-N during periods of reduced water exchange. The net effect of proposed changes is difficult to predict, but it is important to consider that biotic communities far downstream may be affected. Further investigation of algal and nutrient dynamics in the Missouri/Mississippi river system is needed to help guide choices about future management of these resources.

Acknowledgements

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