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Autochthonous and Allochthonous Carbon Cycling in a Eutrophic Flow-Through Wetland

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Abstract Wetland environments are important sites for the cycling and retention of terrestrially derived organic matter and nutrients. Wetland treatment of agricultural runoff has been shown to improve water quality and promote carbon sequestration. However, the potential role of eutrophic wetlands as a source of algal loading contributing to downstream hypoxia has prompted interest in understanding algal productivity and export from these systems. This study, in the San Joaquin Valley, California, quantified a mass balance of carbon and nutrients within a seasonally-saturated constructed wetland receiving agricultural runoff, as well as quantifying autochthonous carbon production on four sampling dates during a year with minimal emergent vegetation. Results from this study show that the wetland was a net-sink for nutrients and particulate/dissolved organic carbon. Despite high concentrations of inflowing nutrients and high rates of primary productivity, high respiration rates limited net organic C production and export due to high heterotrophic activity. The addition of high C loads in inflowing water and moderate retention efficiencies, however, resulted in a positive C retention during most sampling dates. This study provides valuable insight into the connection between elevated carbon and nutrient inflows, their effects on autochthonous carbon production, and resulting carbon and nutrient outflows.

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Introduction

Wetlands provide a critical interface between terrestrial and aquatic environments, regulating the transport of material fluxes to down gradient aquatic ecosystems. These transitional environments are important sites for the retention, production, and export of allochthonous and autochthonous carbon sources (Jordan et al. 2003; O'Geen et al. 2007; Maynard et al. 2011). With nearly half of all wetland habitat lost in the contiguous U.S. by the mid-1980s, the ability of wetlands to serve as buffers between upland and aquatic systems has been greatly diminished, often resulting in widespread degradation of surface water bodies. Wetland losses have been even more dramatic in California's Central Valley, where less than 9 % (~198,000 ha) of the original 2 million ha of wetlands remain (Dahl 1990). Wetland restoration efforts along California's San Joaquin River (SJR), one of two major river systems within the Central Valley (Fig. 1), are gaining attention as a means to mitigate non-point source pollution associated with irrigated agriculture. While constructed wetlands may be effective sinks for suspended solids, nutrients and pesticides (O'Geen et al. 2010), they may also be major sources of oxygen demanding substances (i.e., algal biomass, dissolved organic carbon [DOC], and particulate organic matter) (Tockner et al. 1999). Thus, flow-through wetlands may potentially serve as incubators, transforming nutrients into algal biomass, resulting in no beneficial effect on biological oxygen demand (BOD) loads and dissolved oxygen (DO) concentration in downstream surface waters.
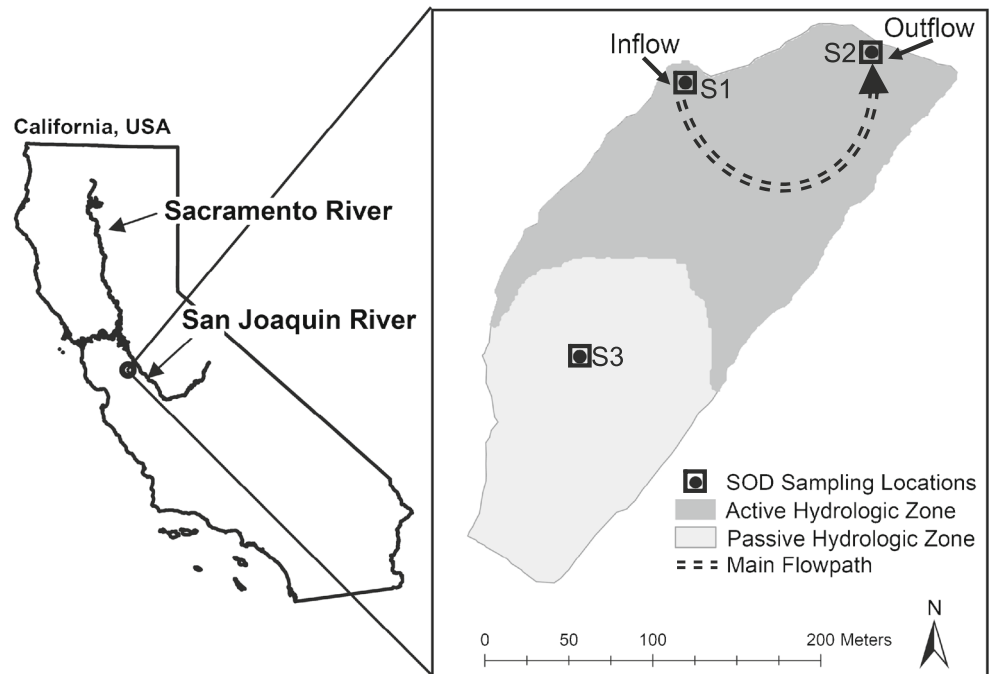
Low DO conditions frequently occur in the lower SJR due to excessive amounts of oxygen demanding substances, principally high algal biomass loading from upstream sources (Volkmar

Fig. 1 Schematic of study site, sediment oxygen demand sampling locations (S1, S2, and S3), inflow and outflow locations, and main flow-path

and Dahlgren 2006). Despite growing interest in using wetlands to intercept agricultural runoff, much is unknown concerning their ability to prevent algal loading and low DO conditions. This is particularly true for seasonally-saturated riparian wetlands of this region that experience annual oscillations between predominately vegetated and non-vegetated states. This annual variation is due to the timing and duration of spring flooding and its subsequent effect on the germination of emergent macrophytes. As a result, many of these constructed wetlands experience years dominated by open water environments, and thus, may become incubators of algal biomass due to high light and nutrient availability combined with long hydrologic residence times. The algal seed source contributed by wetlands can undergo a doubling per day within eutrophic rivers, such as the San Joaquin River, contributing to large increases in BOD during downstream transport (Volkmar and Dahlgren 2006; Ohte et al. 2007; Volkmar et al. 2011). There are currently 72,000 ha of managed seasonally-saturated wetlands in the Central Valley, with the majority of these wetlands receiving high annual loads of nutrients, sediment, and organic carbon (Central Valley Joint Venture 2006). Consequently, growing concern over seasonal hypoxia in the lower reaches of the SJR and the potential role of eutrophic wetlands as a source of algal loading has prompted interest in understanding algal productivity and export from these systems.

To better understand the role of eutrophic wetlands as algal producers, this study calculated a carbon and nutrient mass balance in a seasonally-saturated constructed wetland during an open-water year. Additionally, this study employed a spatially-explicit quantification of aquatic metabolism on four sampling dates during the irrigation season, thus allowing a

mass-balance calculation of autochthonous carbon production. The main objective of this study was to determine the daily mass-balance of autochthonous and allochthonous carbon loads within the wetland, thus allowing us to determine whether the wetland attenuates or amplifies algal loading and carbon export into the San Joaquin River. Specific objectives were to: (i) conduct a mass-balance of wetland organic C; (ii) determine the relative contribution of autochthonous and allochthonous C sources; and (iii) evaluate the effects of elevated carbon and nutrient loading on wetland metabolism and carbon export.

Materials and Methods

Study Area

The study was conducted in a constructed, flow-through wetland located on the west side of the San Joaquin River in California's Central Valley (37.395119, −120.993897). The study site was once part of the historic San Joaquin River floodplain that was converted to agriculture in the 1930's and then restored into a wetland in the early 1990's. The area has a Mediterranean climate with hot dry summers (mean summer temperature of 24 °C) and cool moist winters (mean winter temperature of 8 °C; mean annual precipitation of 28 cm). The wetland is seasonally saturated, receiving agricultural runoff during the summer irrigation season (April–September) from approximately 2,300 ha of irrigated agricultural lands, and rain and flood events in winter and early spring, followed by a brief dry-down period (March–April). This results in a hydroperiod that lasts from 9 to 11 months each year. Soils in the

surrounding agricultural watershed are predominately classified as Calcic Haploxerepts, Typic Haploxerepts, and Mollic Haploxeralfs, with surface soil texture ranging from loams to clay loams. The dominant agricultural crops include alfalfa (*Medicago sativa* L.; 34 % of catchment area), bean (*Phaseolus lunatus* L.; 30 % of catchment area), corn (*Zea mays* L.; 13 % of catchment area), tomato (*Solanum lycopersicum* L.) (9 % of catchment area), walnut (*Juglans regia* L.; 6 % of catchment area), and almond (*Prunus amygdalus*; 5 % of catchment area). This study was conducted during the 2007 summer irrigation season (April-September).

The wetland has an ellipsoidal shape (380 m long, 140 m wide) with a surface area of 4.5 ha and an average water depth of 0.73 m (Fig. 1). Due to early spring flooding in 2007, emergent vegetation (pale smartweed, *Polygonum lapathifolium*) failed to establish resulting in a predominantly open-water environment. Since its construction in 1993, the wetland has oscillated between vegetated (i.e., >70 % plant cover in 1994, 1996, 1999, 2003, and 2004) and non-vegetated (i.e., <10 % plant cover in 1995, 1998, 2000, 2001, 2002, 2005, and 2007) states. The wetland was drained for repair following severe flooding in 1997 and 2006. This type of annual variation in vegetation dynamics is common in seasonally-saturated floodplain wetlands of this region. The studied wetland was found to be functionally similar to other flow-through wetlands in the San Joaquin Valley suggesting that the results of this study may be representative for similar wetlands in the region (Díaz et al. 2012).

Water Budget

A water budget was used to calculate hydrologic fluxes for the study period (April–September, 2007). Water inflow and outflow rates were measured every 15 min using ISCO 2150 (ISCO, Lincoln, NE, USA) area-velocity meters installed in inlet and outlet pipes. Due to minimal plant cover in the wetland, a daily evaporation rate was calculated in place of evapotranspiration using a mass transfer evaporation equation given by Dunne and Leopold (1978). Environmental data were obtained from a local weather station (Patterson, CA; 37.440000, −121.140000) located approximately 15 km from the study wetland and maintained by the California Irrigation Management Information System (CIMIS 2007). There was no recorded precipitation during the study period. Seepage was calculated as: Seepage= Inflow−(Outflow+Evaporation).

To account for deviations from plug flow conditions, active (i.e., area surrounding the main flow path) and passive (i.e., backwater region) hydrologic zones were estimated within the wetland (Maynard et al. 2009b). The delineation of each hydrologic zone was accomplished through observation of both flow path and sedimentation patterns. Due to the close proximity of inflow and outflow structures in the northern

portion of the wetland, significant hydrologic short-circuiting occurs within the northern section, creating distinct hydrologic environments between the northern and southern sections (Fig. 1). The wetland has an average water volume of 32,700 m³ and an average inflow rate of 9,720 m³ d⁻¹, resulting in a nominal residence time of 4.0 days (range: 2.6 to 6.7 days). However, moment analysis of the residence time distribution (RTD) (Levenspiel 1972), calculated from a bromide tracer study conducted on 06 August, 2007, revealed that the wetland has an effective residence time of 0.90 days at the median inflow rate of 8,300 m³ d⁻¹ (variance: 18.6 days) (Table 1). The variance of the effective residence time indicates the degree of short-circuiting within the wetland and is calculated from the second moment of the RTD (Levenspiel 1972).

Inflow and Outflow Carbon and Nutrient Mass Balance

Weekly grab samples (2 L) were collected from the top 30 cm of water column in acid-washed polyethylene bottles from inflow and outflow locations during the 2007 irrigation season (April-Sept; n=20). Electrical conductivity (EC) was measured with a Fisher Accumet AB30 conductivity meter (Fisher Scientific, Pittsburgh, PA, USA) and reported on a standardized 25 °C basis. Turbidity was measured and reported as NTU (Nephelometric Turbidity Unit) using a Hach 2100P turbidimeter (Hach, Loveland, CO, USA). Total suspended solids (TSS) was measured by filtration through a 0.45 μm pre-combusted, pre-weighed glass fiber filter (Millipore) with a limit of detection (LOD) of ~0.5 mg L⁻¹. The filter was dried at 60 °C for 24 h and weighed again, the difference giving TSS. The filter was further combusted at 550 °C for 3 h with

Table 1 Wetland characteristics and hydrologic data during the summer irrigation season (April-Sept) in 2007

Inflow (m³)	1,422,208	100%[a]
Outflow (m³)	1,233,933	86.8%[a]
Evapotranspiration (m³)	20,233	1.4%[a]
Seepage (m³)	153,287	11.8%[a]
Mean Wetland Area (m²)	44,798	
Mean Wetland Volume (m³)	32,700	
Mean Wetland Depth (m)	0.73	
Mean Inflow Rate (m³ d⁻¹)	9,720	
Active Hydrologic Area (m²)	~20,000	
Nominal Residence Time (days)	4.0	
Effective Residence Time (days)	0.90±18.6[b]	
Flow Path Length (m)	250	

[a] Percent of total flow

[b] Effective residence time calculated from tracer study±variance. Variance calculated from the second moment of the residence time distribution

the difference in mass giving volatile suspended solids (VSS) (i.e., organic matter) (APHA 1998). VSS values were converted to particulate organic carbon (POC) using a previously established C: VSS ratio of 0.194 (std. error=0.009) for the study wetland (Maynard et al. 2011). The POC fraction includes both autochthonous (e.g., algal C) and allochthonous (e.g., soil organic C) carbon sources. Chlorophyll-a (Chl-a) was measured using ethanol extraction and standard fluorometry techniques (APHA 1998). Chlorophyll-a values were converted to algal-carbon using a C: Chl ratio of 40:1 (Lehman et al. 2004). Total phosphorus (TP) and total nitrogen (TN) were measured following persulfate digestion of a non-filtered sample (APHA 1998).

A subsample was filtered through a 0.2 μm polycarbonate membrane (Millipore) for quantification of dissolved reactive phosphorus (DRP), nitrate-N (NO_3-N), ammonium (NH_4-N), and dissolved organic carbon (DOC). TP and DRP were measured using the ammonium molybdate spectrophotometric method (LOD~5 μg L^{-1}; APHA 1998). TN and NO_3-N were measured using the vanadium (III) chloride method (LOD~10 μg L^{-1}; Doane and Horwath 2003). NH_4^+-N was determined spectroscopically with the Berthelot reaction, using a salicylate analog of indophenol blue (LOD~10 μg L^{-1}; Forster 1995) . DOC was measured using a Dohrmann UV enhanced-persulfate TOC analyzer (LOD= 0.1 mg L^{-1}; Phoenix 8000). Constituent loads were estimated using the period-weighted approach with weekly constituent concentration and weekly water flux (Moldan and Cerny 1994).

Autochthonous Carbon Calculations

The procedure for calculating a spatially contiguous estimate of aquatic metabolism has been described in detail elsewhere (Maynard et al. 2012). Briefly, gross primary productivity (GPP) and community respiration (CR) were determined using a modification of the one-station diel dissolved oxygen (DO) change method, the difference between GPP and CR equaling net ecosystem production (NEP) (Odum 1956; Odum and Hoskin 1958). Spatially-explicit sampling of DO, EC, temperature, turbidity, and fluorescence (a proxy for Chl-a) were conducted with YSI 6600 multiparameter sondes (Yellow Springs Instruments, Yellow Springs, OH, USA), recorded at a constant water column depth (~0.4 m), and calibrated according to manufacturer's instructions before each deployment. Fluorescence values were converted to Chl-a (μg L^{-1}) based on a field-established regression equation developed for this wetland site (r^2=0.92, p <0.001, n = 16). Sondes were interfaced with a Global Positioning System (GPS; Garmin Rino 120; WAAS enabled; Garmin International Inc., Olathe, KS, USA) and used to rove across the wetland logging position and water quality parameters every 10 m on average. There were four sampling campaigns during

the 2007 irrigation season (06 June, 11 July, 15 August, 13 September), with each campaign consisting of three consecutive spatial sampling events over a two-day period: dusk-Day 1, dawn-Day 2, and dusk-Day 2. For each spatial sampling event, ~300 georeferenced data points were recorded and used to interpolate the spatial distribution of DO, Chl-a, turbidity, temperature and EC at unsampled locations. All metabolism calculations were conducted using spatially interpolated values for each water column parameter (i.e., DO, temp), resulting in 44,798 contiguous 1 m grid values across the wetland. The wetland water column was maintained at a constant depth throughout the irrigation season via a water control structure at the outflow. Water column depth was measured using a meter stick (accuracy: ±0.01 m) with a round plexi-glass disc attached at the bottom to prevent insertion into the loose wetland surface sediment. Water column depth was measured at 75 points within the wetland using a non-aligned grid sampling design and recorded values were used to interpolate water depth at all unsampled locations. Reaeration coefficients were determined using the floating diffusion dome method (Copeland and Duffer 1964). Volumetric rates were converted to areal units (g O_2 m^{-2} day^{-1}) by multiplying by the depth of the water column. For comparison to water column C measurements, metabolism measurements were converted to C units following Bott (2006).

Sediment Oxygen Demand

Sediment oxygen demand (SOD) chambers were constructed based on a design by Murphy and Hicks (1986), with slight modifications (Rounds and Doyle 1997; Wood 2001). The SOD chamber was constructed from the top of a 210 L plastic barrel, which enclosed 116 L and exposed a 0.268 m^2 area of sediment. Each chamber was fitted with a bilge pump to recirculate water from the main chamber through three flow diffusers. A YSI 556 multiparameter sonde was connected to each chamber through a sealed port and continuous measurements of DO and temperature were logged at 1-min intervals over a period of 1–2 h. SOD chambers were carefully placed in the wetland sediment to minimize sediment resuspension. SOD was calculated based on the regression line describing the change in O_2 concentration over time:

$$SOD_T = 1.44 \frac{V}{A} b$$

where SOD_T is the sediment oxygen demand (g O_2 m^{-2} d^{-1}) at temperature T, b is the slope of the regression (mg L^{-1} min^{-1}), V is the volume of the chamber (L), A is the area of sediment covered by the chamber (m^2), and 1.44 is a factor for unit conversion. A total of eight SOD measurements were taken at the following three sites (S1, S2, and S3) during the course of the 2007 sampling season: S1 on 06 June, 11 July, 15 August,

and 13 September; S2 on 11 July and 13 September; and, S3 on 15 August and 13 September: (Fig. 1). Dates with a single measurement are reported as that value, while dates with multiple measurements are reported as the mean value±standard deviation.

Data Analysis

Statistical and geostatistical analyses were conducted using R software (R Development Core Team 2009). All spatial interpolation was conducted using ordinary kriging (Goovaerts 1999). Kriging analysis was performed with the "gstat" package (Pebesma 2004). Variogram fitting for each variable was optimized using iterative re-weighted least squares using the "automap" package (Hiemstra et al. 2009). Pairwise Wilcoxon Rank Sum Test was used to compare statistical differences between inflow and outflow nutrients, sediment and carbon loads. Statistical differences were tested at $p = 0.01$ unless otherwise noted and adjusted using Bonferroni correction.

Results

Wetland Carbon, Nutrient and Sediment Mass Balance

Seasonal water flux during the 2007 irrigation season was 1.42 and 1.23 million m^3 at inflow and outflow locations, respectively. The outflow water flux accounted for 86.8 % of inflow volume, with evaporation (1.4 %) and seepage (11.8 %) accounting for the remainder (Table 1). Nutrient, sediment and carbon outflow loads were significantly ($p < 0.01$, except DOC: $p < 0.05$) lower than inflow loads, with the exception of Chl-a which was significantly higher at the outflow. Seasonal sediment load was 364,443 kg at the inflow

and 73,104 kg at the outflow, resulting in 80 % retention of suspended sediment (Table 2). The average particle size distribution of TSS was previously reported as 13 % sand, 53 % silt, and 34 % clay for in-flowing TSS; and 6 % sand, 32 % silt and 62 % clay for out-flowing TSS (Maynard et al. 2009b). Net seasonal retention of POC was 46 %, with an inflow load of 5,876 kg and an outflow load of 3,155 kg. Smaller reductions in DOC load between inflow (6,786 kg) and outflow (5,906 kg) occurred, resulting in a 13 % decrease in outflow load, likely due to loss via seepage (11.8 % seepage). This implies that there was little to no biodegradation of DOC within the wetland. High algal productivity within the wetland resulted in a 7-fold increase (386 to 3,038 kg) in algal C load between the inflow and outflow (Table 2). A noticeable spike in algal C load at the outflow occurred on 22 July, coincident with a drop in TSS load. In general, nutrient load retention efficiencies were low, with 26 % retention of TN and 36 % retention of TP. Nitrate-N had the lowest seasonal retention (19 %), while NH_4-N had the highest (64 %). The NO_3-N inflow load, however, was an order of magnitude higher than NH_4-N inflow load (NO_3-N: 6,833 kg vs. NH_4-N: 472 kg). Seasonal retention of DRP was similar to TP, with a 39 % load reduction.

Intra-Seasonal Variation in Wetland Chemical and Physical Parameters

In general, daily inflow nutrient loads were higher than daily outflow nutrient loads, with loads fluctuating only slightly during the irrigation season. Dissolved reactive P loads closely followed patterns of TP and NO_3^- loads closely followed patterns of TN. Ammonium inflow and outflow loads were negligible during the irrigation season (Fig. 2a–e). Daily inflow loads of TSS were high and fluctuated considerably

Table 2 Wetland sediment, carbon and nutrient loads at inflow and outflow locations during the summer irrigation season (April-Sept) in 2007. Constituent loads were calculated using continuous flow data and 20 weekly grab samples

		Inflow	Outflow	Net Retention	
		kg season^{-1}	kg season^{-1}	kg ha^{-1} season^{-1}	%
Total Suspended Solids	TSS	364,443[a][a]	73,104[b]	65,031	80
Particulate Organic Carbon	POC	5,867[a]	3,155[b]	605	46
Dissolved Organic Carbon	DOC	6,786[a]	5,906[b]	196	13
Chlorophyll-a	Chl-a	9.7[a]	75.9[b]	−15	−687
Algal Carbon	Algal-C	386[a]	3,038[b]	−592	−687
Total Nitrogen	TN	8,741[a]	6,448[b]	512	26
Nitrate-N	NO$_3$-N	6,833[a]	5,540[b]	289	19
Ammonium-N	NH$_4$-N	472[a]	169[b]	68	64
Total Phosphorus	TP	493[a]	317[b]	39	36
Dissolved Reactive Phosphorus	DRP	256[a]	157[b]	22	39

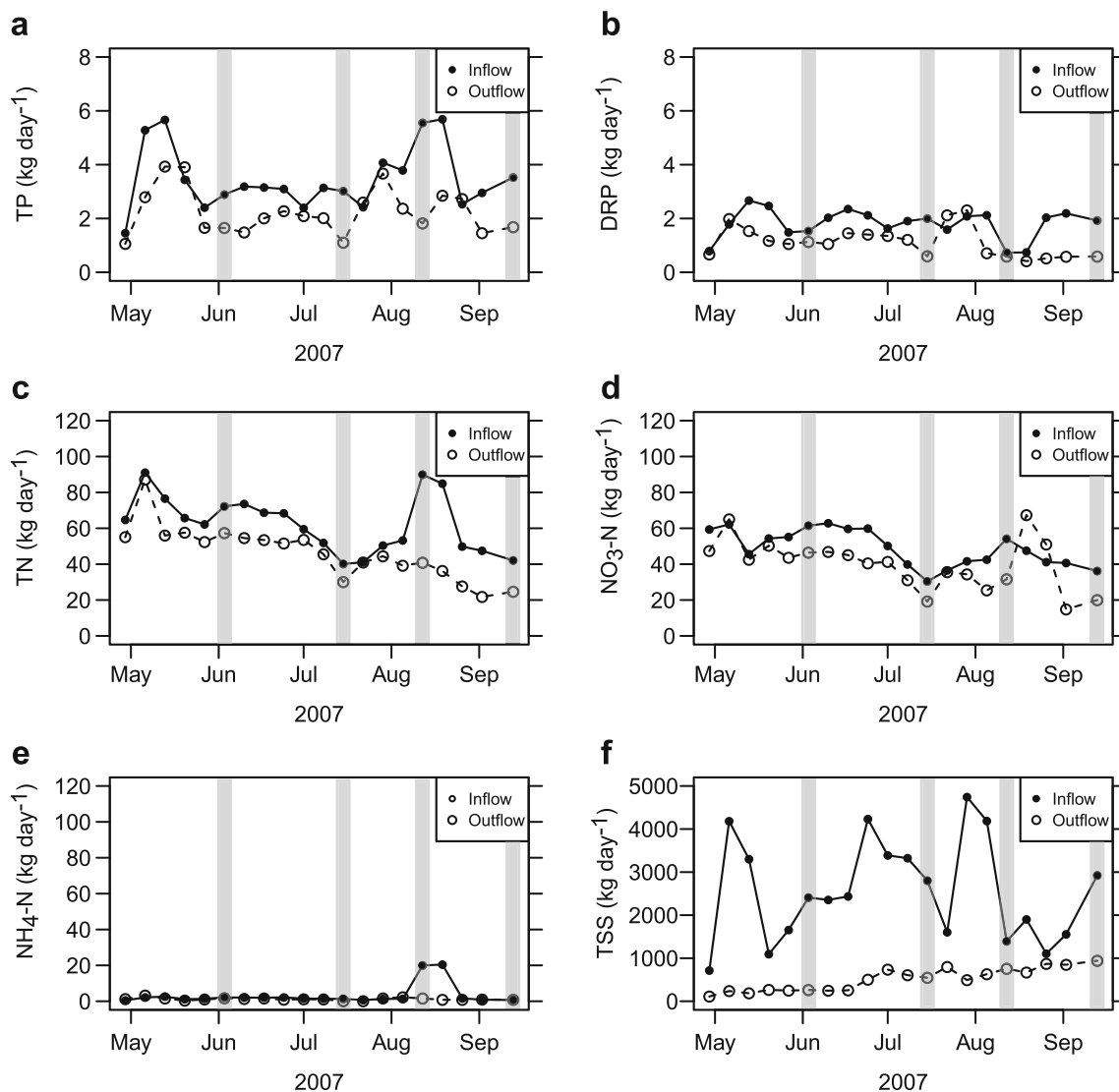[a] Letters indicate significant ($p < 0.01$) differences between inflow and outflow

Fig. 2 Wetland daily nutrient loads for (**a**) total phosphorus, (**b**) dissolved reactive phosphorus, (**c**) total nitrogen, (**d**) nitrate, (**e**) ammonium, and (**f**) total suspended solids. Shaded areas designate the four seasonal sampling campaigns

throughout the irrigation season, with a mean seasonal daily load of 2,546±1,225 kg day^{-1} ($\bar{x}$ ± std. dev.). Total suspended solids daily outflow loads were consistently low, with a mean seasonal daily load of 487±251 kg day^{-1} (Fig. 2f).

The fate of organic carbon in the water column was assessed through measurements of POC, DOC, and algal-C daily loads at inflow/outflow locations. In general, trends in daily inflow POC loads were similar to inflow TSS loads, with considerable fluctuations during the irrigation season. Daily outflow POC loads were generally low, with the exception of a spike in POC loading in late July that corresponded with a spike in algal-C loads (Fig. 3b & d). Daily inflow and outflow DOC loads were relatively constant during the irrigation season (Fig. 3c). Trends in daily algal-C loads were significantly higher at the outflow relative to the inflow, indicating that the wetland was a net source of algal biomass (Fig. 3d). Average

daily algal-C loads were 2.7±1.5 kg d^{-1} at the inflow and 21.6±30.9 kg d^{-1} at the outflow.

Daily water, sediment and nutrient inflow loads on each of the four sampling campaigns during the 2007 irrigation season are presented in Table 3. In general, these four sampling dates were representative of the intra-seasonal variation in nutrient, carbon and sediment loading. Daily hydrologic loads were ~12,000 m^3 d^{-1} early in the irrigation season (06 June), but decreased to approximately 8,000 to 9,000 m^3 d^{-1} for the remainder of the season (Table 3, Fig. 3a). Daily nitrogen inflow loads fluctuated with no clear temporal trend. In contrast, daily TP and DRP loads were relatively constant throughout the season, with the exception of 15 August when TP was unusually high (5.41 kg d^{-1}) and DRP unusually low (0.70 kg d^{-1}) (Table 3, Fig. 3a and b).
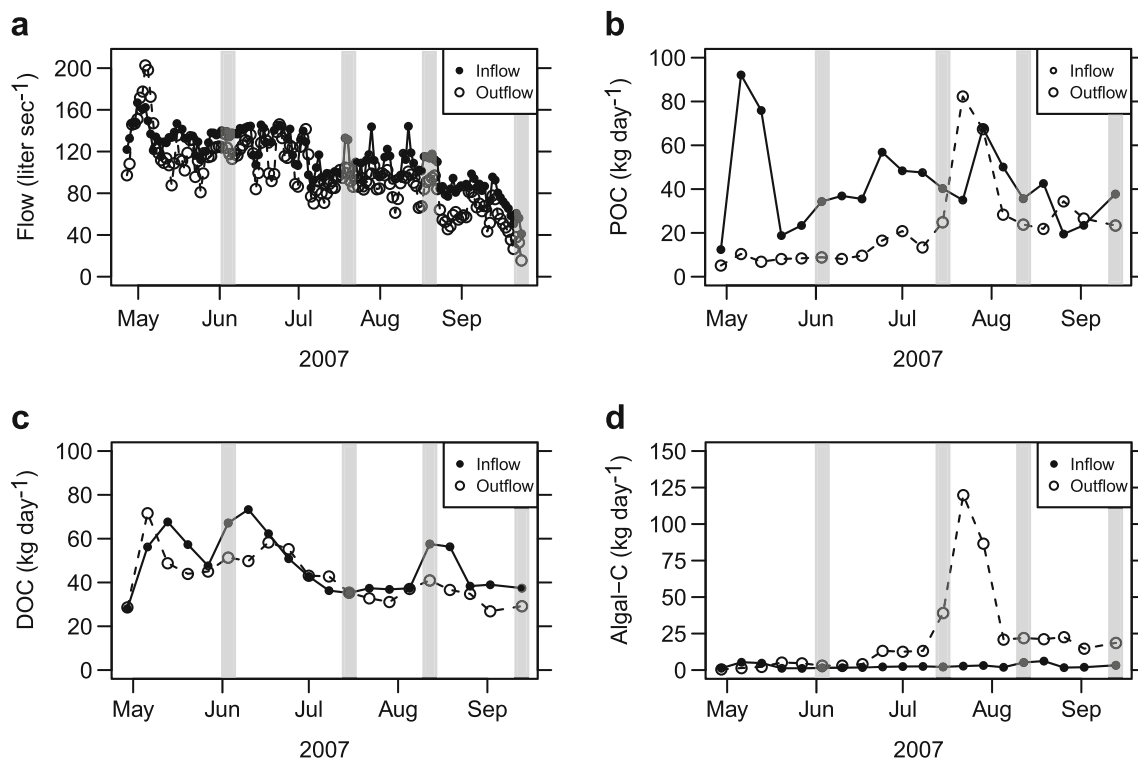
Fig. 3 Wetland daily flow rate (**a**), and wetland daily carbon loads for (**b**) particulate organic carbon, (**c**) dissolved organic carbon, and (**d**) algal carbon. Shaded areas designate the four seasonal sampling campaigns

EC was relatively constant with most values fluctuating around 1000 μS cm^{-1} and pH of 8 (Table 3). Turbidity was highly variable with mean daily values ranging from 31.6 NTU (06 June) to 116.6 NTU (11 July). Reaeration coefficients calculated from diffusion dome measurements were consistently low with K_{O2} values ranging from 0.74 to 2.66 d^{-1} (Table 3). Rates of SOD were relatively constant during the season, with rates ranging from 2.51 to 5.16 g O$_2$ m^{-2} d^{-1} (Table 3). SOD rates were also relatively consistent across the three sampling sites, which were representative of the different hydrologic, biogeochemical, and depositional environments within the wetland. Rates of sediment oxygen consumption were statistically indistinguishable between sampling periods. Another potential contributor to oxygen consumption is via nitrification with a loss of 4.33 g O$_2$ per g of NH$_4$-N (Wezernak and Gannon 1967). If we assume that all NH$_4$-N retained in the wetland was converted to nitrate it would account for 1.5, 0.3, 18.5 and 0.0 % of O$_2$ consumed in our CR estimates on 06 June, 11 July, 15 August, and 13 September, respectively (Table 3). Thus in general, potential nitrification would account for a very small percentage of O$_2$ consumption in our wetland, with the exception of 15 August when inflowing NH$_4$-N load was an order of magnitude higher than previous or subsequent NH$_4$-N loads during the sampling season (Fig. 2e).

Partitioning Autochthonous and Allochthonous Wetland Carbon Sources

A daily mass balance of allochthonous and autochthonous C sources was calculated within the wetland during the four sampling campaigns (Table 4). Allochthonous C entered the wetland via inflowing agricultural runoff in both particulate and dissolved forms. Daily imported POC loads were relatively constant throughout the season, with a seasonal mean of 41.9±20.4 kg d^{-1} (Fig. 3b). During the four sampling campaigns, daily POC inflow loads ranged from 37.1 (06 June) to 42.9 kg C d^{-1} (11 July). Daily imported DOC loads ranged from 36.7 (11 July) to 72.0 kg C d^{-1} (06 June) (Table 4). Algal C comprised a very small fraction of total imported C (1–2 %), indicating that the majority of imported C is likely of terrestrial origin (e.g., soil organic matter). Additionally, particulate carbon entering the wetland had a C:N ratio of ~9, further indicating a predominance of soil organic matter and particulate plant material, and lesser amounts of algae (Maynard et al. 2011). Autochthonous carbon production (GPP-C) was low at the beginning and end of the season, with daily loads of 89.7 kg C d^{-1} on 06 June and 93.2 kg C d^{-1} on 13 September. Daily loads increased dramatically during peak summer sampling dates, with a peak load of 191.7 kg C d^{-1} on 15 August (Table 4). Autochthonous C loads were more than five times higher than allochthonous loads during the peak of summer, in contrast to the beginning and end of the season when loads

Table 3 Wetland daily water fluxes, sediment and nutrient loads, and environmental parameters in 2007. Values are reported as either the mean or mean ±standard deviation

Parameter[a]	Units	Sampling Date			
		06 June	11 July	15 Aug.	13 Sept.
Inflow Water Flux	$m^3 \, d^{-1}$	11,780	8,571	8,836	8,011
Sediment-Influx	$kg \, d^{-1}$	2,311	2,923	1,806	2,924
TN-Influx	$kg \, d^{-1}$	72.2	41.9	80.7	42.1
NO_3-Influx	$kg \, d^{-1}$	61.7	31.7	45.2	36.2
NH_4-Influx	$kg \, d^{-1}$	2.02	1.32	19.43	0.69
NH_4-Outflux	$kg \, d^{-1}$	1.27	1.05	0.65	0.86
TP-Influx	$kg \, d^{-1}$	3.13	3.15	5.41	3.52
DRP-Influx	$kg \, d^{-1}$	1.99	2.08	0.70	1.92
EC[b]	$\mu S \, cm^{-1}$	997±2	797±2	961±12	1035±3
Turbidity[b]	NTU	31.6±6.1	116.6±17.5	67.2±6.9	116.6±6.8
Wind Speed	$m \, s^{-1}$	4.3±2.2	3.1±1.0	2.2±1.5	2.2±1.0
Wind Direction	0–360°	273±90	287±130	297±81	226±107
Water Temperature[b]	°C	21.1±0.2	26.4±3.0	25.3±1.6	23.5±1.3
SOD	$g \, O_2 \, m^{-2} \, d^{-1}$	2.55	3.58±2.09	5.16±0.29	3.51±1.20
Daily PAR	$E \, m^{-2} \, d^{-1}$	59.7	56.1	50.2	42.5
K_{O2}-Dome	d^{-1}	1.98±0.64	2.66±1.33	1.09±0.60	0.74±0.38
GPP[b]	$g \, O_2 \, m^{-2} \, d^{-1}$	6.41±0.91	9.08±1.42	13.69±3.36	6.66±1.06
NEP[b]	$g \, O_2 \, m^{-2} \, d^{-1}$	0.56±0.38	1.05±1.08	2.42±0.73	0.35±0.40
CR[b]	$g \, O_2 \, m^{-2} \, d^{-1}$	4.85±1.16	7.68±3.19	9.79±3.22	6.10±1.05
$CR_{Nitrification}$[c]	$g \, O_2 \, m^{-2} \, d^{-1}$	0.07 (1.5 %)	0.03 (0.3 %)	1.81 (18.5 %)	0 (0 %)
GPP:CR	ratio	1.42	1.18	1.40	1.09
DO_{Dawn}[b]	$mg \, L^{-1}$	6.06±0.46	7.28±0.57	7.42±1.38	6.11±0.36
DO_{Dusk}[b]	$mg \, L^{-1}$	9.73±0.36	13.47±1.15	17.63±1.29	10.79±0.88
Chl-a[b]	$\mu g \, L^{-1}$	3.0±2.0	37.6±5.5	60.0±5.1	18.1±4.1

[a] TN, total nitrogen; TP, total phosphorus; DRP, dissolved reactive phosphorus; EC, electrical conductivity; SOD, sediment oxygen demand; PAR, Photosynthetically active radiation; K_{O2}-Dome, reaeration coefficients calculated using floating diffusion dome; GPP, gross primary productivity; NEP, net ecosystem production; CR, community respiration; DO, dissolved oxygen; Chl-a, chlorophyll-a

[b] Mean values from spatial sampling comprising 44,798 interpolated points

[c] Oxygen consumption assuming all retained NH_4-N is nitrified at an O_2:NH_4-N ratio of 4.33. Percentage of CR that is potentially due to nitrification is shown in parentheses

were similar. The seasonal pattern of daily gross C additions (autochthonous+allochthonous) were largely determined by patterns of autochthonous production, with low loads at the beginning and end of the season and high loads during the middle of the season (Table 4).

Wetland C losses consisted of C exported in outflow, C respired within the wetland, and DOC lost via seepage. Exported POC loads were low relative to imported POC, with a mean daily load of 22.4±20.5 kg d^{-1} and daily values during the four sampling campaigns ranging from 8.8 to 24.6 kg C d^{-1}. Exported DOC loads were significantly lower than imported DOC, with a mean daily load of 42.9±11.2 kg d^{-1} and daily values during the four sampling campaigns ranging from 29.2 to 48.8 kg C d^{-1}. The reduction in DOC load, however, can be accounted for by seepage (Tables 1 and 4).

The mean daily exported algal C load was 21.6±30.9 kg d^{-1} and ranged from 3.0 (06 June) to 37.3 kg C d^{-1} (11 July) during the four sampling campaigns. Carbon respired within the wetland (CR-C) followed the same seasonal pattern as GPP-C, with loads ranging from 69.3 to 139.8 kg C d^{-1}. Carbon respiration associated with the wetland sediment (SOD-C) ranged from 47 to 57 % of total respired C, with SOD-C loads ranging from 36.4 to 73.7 kg C d^{-1}. The seasonal pattern of daily gross C losses (exported+respired) were largely determined by seasonal patterns of C respiration, with low loads at the beginning and end of the season and high loads during the middle of the season (Table 4).

Net C storage (Net-C) was highly variable throughout the season with daily loads ranging from 28.3 kg to 75.1 kg C d^{-1}. Net retention of C based on import–export fluxes (Net-Flux)

Table 4 Daily mass balance of allochthonous and autochthonous carbon sources on four sampling dates during the 2007 growing season

Parameters[a]	Sampling Date			
	06 June kg C day⁻¹	11 July	15 Aug.	13 Sept.
Wetland Carbon Additions				
Allochthonous Carbon Import				
POC	37.1	42.9	41.3	37.8
DOC	72.0	36.7	53.5	37.4
Algal-C[b]	1.6	2.3	5.9	3.3
Autochthonous Carbon Production				
GPP-C	89.7	127.0	191.7	93.2
Algal-C[b]	12.5	91.4	74.5	28.4
Gross Carbon Addition				
Tot-C[c]	198.8	206.6	286.5	168.4
Wetland Carbon Losses				
Carbon Export				
POC	8.8	24.6	18.3	23.6
DOC	48.8	33.7	29.2	29.4
Algal-C[b]	3.0	37.3	16.9	18.8
Respired Carbon				
CR-C	69.3	109.7	139.8	87.15
SOD-C	36.4 (53 %)	51.1 (47 %)	73.7 (53 %)	50.1 (57 %)
Gross Carbon Loss				
Loss-C[c]	126.9	168.0	187.3	140.2
Daily Net Carbon Balance				
Net-Flux[d]	51.5	21.4	47.3	22.3
NEP-C	20.4	17.3	51.9	6.0
Net-C[c]	71.9	36.6	99.2	28.3

[a] POC, particulate organic carbon; DOC, dissolved organic carbon; GPP-C, gross primary production converted to carbon units; CR-C, community respiration converted to carbon units

[b] Algal-C determined from chlorophyll-a concentrations in inflow, outflow and across the water column at one point in time and are use to show relative differences across the field season

[c] Tot-C is the sum of inflow POC, inflow DOC, and GPP-C; Loss-C is the sum of outflow POC, outflow DOC and CR-C; Net-C is the difference Tot-C and Loss-C

[d] Net-Flux is the difference between imported C (inflow-POC+ inflow-DOC) and exported C (outflow-POC+outflow-DOC)

ranged from 21.4 to 51.5 kg C d⁻¹, comprising between 69 and 100 % of daily net C storage (Net-C). Carbon associated with NEP ranged from 6.0 on 13 September to 51.9 kg C d⁻¹ on 15 August (Table 4).

Discussion

Wetland Carbon and Nutrient Mass Balance

Floodplain wetlands serve a vital role in agricultural landscapes through regulating material fluxes between terrestrial and aquatic environments. High rates of organic C and nutrient loading from agricultural watersheds have fundamentally changed the magnitude and rate of resource processing in wetland systems. This study quantified a mass balance of carbon and nutrients within the wetland, as well as quantifying autochthonous carbon production on four sampling dates during the irrigation season. While previous studies have documented inflow and outflow carbon loads (Braskerud 2001; Jordan et al. 2003; O'Geen et al. 2007; Maynard et al.

2009a), there have been no mass balance studies of autochthonous carbon production and cycling and its effect on wetland carbon export. Thus, this study provides valuable insight into the connection between elevated carbon and nutrient inflows, its effect on autochthonous carbon production, and resulting carbon and nutrient outflows.

Results from the wetland C mass balance illustrate the high retention capacity of the wetland in terms of POC, and to a lesser degree DOC. The contribution of algal-C to output loads of POC increased substantially during mid-summer sampling dates (Table 4, Fig. 3), which in turn decreased the percent reduction in outflow C loads. This was most noticeable on 22 July when outflow Algal-C load increased an order of magnitude with a concomitant increase in outflow POC load (Fig. 3). This dramatic increase in algal biomass was also coincident with a sharp decrease in TSS, implicating improved light conditions as a possible reason for the increased wetland productivity (Table 3). After accounting for the addition of allochthonous C inputs and autochthonous/ allochthonous outputs, the daily net C sequestration was positive on all sampling dates. This is in agreement with a

previous study in this system that showed significant seasonal enrichment of deposited sediment and organic C within the wetland (Maynard et al. 2011).

Autochthonous and Allochthonous Carbon Loads

The balance between GPP and CR (i.e., aquatic metabolism), provides an important indicator of ecosystem function in response to environmental change. The ratio of GPP to CR (GPP:CR) is used extensively as an indication of wetland trophic status, where ecosystems are classified as either autotrophic (i.e. net producer of C, GPP:CR>1) or heterotrophic (i.e., net consumer of C, GPP:CR<1) (López-Archilla et al. 2004; Iwata et al. 2007). Overall, the GPP/CR ratio was close to 1 (range: 1.09–1.42), indicating the important role of the autotrophic community in maintaining positive rates of NEP, as well as the important role of the heterotrophic community in regulating NEP in a system with high rates of GPP (Table 3). Thus, large inputs of allochthonous POC during peak periods of GPP (i.e., 11 July) likely contribute to increased heterotrophic energy mobilization, limiting net ecosystem production (NEP) and the potential export of BOD loads (Table 4). Allochthonous C inputs can play an important role in whole ecosystem metabolism, with inputs that can equal or exceed internal primary productivity (Hynes 1970; Cummins et al. 1973; Fisher and Likens 1973; Caraco and Cole 2004; Cole et al. 2006). For example, many lake ecosystems experience negative NEP due to high respiration rates, but maintain a positive net C storage due to the high influx of allochthonous C (Del Giorgio and Peters 1994; Del Giorgio et al. 1999; Cole et al. 2000). In our study wetland we documented a similar trend, with low rates of NEP due to high respiratory demand; but a substantial positive carbon balance in the system due to high inputs of allochthonous POC..

Autochthonous C is considered relatively labile and easily metabolized, in contrast to allochthonous sources which are considered largely recalcitrant (Wetzel 1992). Results from bioassays on the short-term lability of DOC in lakes suggest that less than 15 % of terrestrial DOC is available for microbial use (Sondergaard et al. 1995; Volkmar and Dahlgren 2006). However, recent studies have shown that allochthonous C is important in subsidizing aquatic food webs in lake ecosystems, with 30–70 % of organismal C originating from terrestrial sources (Carpenter et al. 2005; Cole et al. 2006; Karlsson et al. 2002; Pace et al. 2004). Additionally, greater than 90 % of ecosystem decomposition in rivers and lakes is estimated to originate from non-pelagic sources (Wetzel 1992). The high influx of POC in this wetland, and its active recirculation as a result of resuspension, results in the continual exposure of allochthonous POC to metabolic processing. Furthermore, deposited C on the wetland floor is subjected to benthic metabolism, which has been shown to account for as much as 50 % of total O_2 consumption in rivers (Hanes and Irvine 1968) and as much as 80 % of total O_2 consumption in lakes (Burns and Ross 1972). SOD in our system was relatively constant throughout the season as well as across sampling sites, with the relative contribution of SOD to total O_2 consumption ranging from 47 to 57 % of total areal O_2 consumption. It should be noted that the limited number of SOD measurements taken both at individual sites and throughout the season, results in an approximate average estimate of SOD within the wetland. Despite this caveat, estimated areal rates provide an approximation of the relative contribution of SOD to total respiratory demand (Table 4).

Effect of Elevated Nutrient, Carbon, and Sediment Loads on Wetland Metabolism

The balance between heterotrophic and autotrophic energy mobilization is largely controlled by the ratio of allochthonous organic C to inorganic nutrients (Blomqvist et al. 2001; Cole et al. 2002; Jansson et al. 2006). In systems with high availability of organic C relative to inorganic nutrients, bacterioplankton will outcompete phytoplankton for limiting nutrients (e.g., P and N) (Vadstein 2000). In contrast, low organic C availability relative to inorganic nutrients will favor phytoplankton productivity due to the dependence of bacterioplankton on an external C source. Our study revealed temporal patterns of wetland aquatic metabolism typical of seasonal fluctuations in temperature and irradiance. High C loads entering our wetland prevented C limitation. Thus, regulation of phytoplankton and bacterioplankton growth was likely controlled by light availability, temperature, and nutrients (i.e., N and P). A concurrent study in this wetland showed that GPP was most strongly correlated with turbidity and NEP was most strongly correlated with DRP (Maynard et al. 2012). The resuspension of sediment organic C has also been shown to be an important factor in regulating CR (Bachmann et al. 2000). Sediment resuspension was a major source of turbidity in our wetland, which limited light availability for algal growth, while at the same time, potentially increasing C and nutrient availability for heterotrophic bacteria, resulting in a general shift of the system towards heterotrophic metabolism (Maynard et al. 2012). Additionally, bacterioplankton growth and respiration is dependent on temperature, resulting in lower rates of CR during colder months (Uehlinger et al. 2000), as seen on 06 June and 13 September (Table 3). This relationship between CR and temperature was also shown in a concurrent study in this system, where CR was most strongly correlated with temperature (Maynard et al. 2012).

With the increasing use of constructed and restored riparian wetlands for mitigating sediment and nutrient loads from agricultural runoff, it is important to also evaluate their potential role as algal seed sources for down gradient water bodies. This is particularly relevant for seasonally-saturated riparian

wetlands of this region that experience annual oscillations between predominately vegetated and non-vegetated states. This study documented wetland algal dynamics during a non-vegetated year and showed a highly significant increase in algal carbon exported from the system. While the overall carbon budget showed a positive net retention of carbon within the system, it appears that the high retention of imported allochthonous carbon is being partly offset by the high production of algal C, part of which is being exported from the system. Previous work in this system during a vegetated year documented moderate Chl-a concentrations in spring during early stages of emergent macrophyte growth, followed by extremely low Chl-a concentrations due to shading by the fully established vegetative canopy (O'Geen et al. 2007). Thus it appears that promoting the establishment of wetland vegetation may be an effective management practice for reducing algal productivity, however, further research is needed to evaluate the effects of wetland vegetation on algal export loads.

Conclusions

The widespread degradation of surface water bodies, coincident with dramatic losses of wetland habitat, has prompted interest in using constructed and/or restored wetlands to mitigate non-point source pollution. While constructed wetlands have been shown to be effective at retaining sediment and nutrients, less is known regarding their effect on algal productivity and export. Results from this study show that: (i) the wetland had a high retention capacity for sediment, nutrients and POC; (ii) despite high rates of primary productivity (GPP), high respiration rates (CR) limited net C production (NEP) and export from this wetland; and (iii) while there was a net retention of C within the system, the high retention of imported allochthonous carbon is being partly offset by the production and partial export of algal C. Consequently, additional research evaluating management practices that minimize algal productivity within constructed flow-through wetlands (i.e., vegetation) should be examined in an ongoing effort to mitigate seasonal hypoxia in the SJR and other water bodies.

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