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Temporal variation in organic carbon spiraling in Midwestern agricultural streams

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Abstract Inland freshwaters transform and retain up to half of the carbon that enters from the terrestrial environment and have recently been recognized as important components of regional and global carbon budgets. However, the importance of small streams to these carbon budgets is not well understood due to the lack of globally-distributed data, especially from streams draining agricultural landscapes. We quantified organic carbon pools and heterotrophic metabolism seasonally in 6 low-order streams draining row-crop fields in northwestern Indiana, USA, and used these data to examine patterns in organic carbon spiraling lengths (S_{OC}; km), downstream velocities (V_{OC}; m/d), and turnover rates (K_{OC}; day^{-1}). There were seasonal differences in S_{OC}, with the longest spiraling lengths in winter (range: 7.7–54.4 km) and the shortest in early and late summer (range: 0.2–9.0 km). This seasonal pattern in S_{OC} was primarily driven by differences in discharge, suggesting that hydrology tightly controls the fate of organic carbon in these streams. K_{OC} did not differ seasonally, and variability (range: 0.0007–0.0193 day^{-1}) was controlled by differences in stream water soluble reactive phosphorus concentrations. Compared to previous studies conducted primarily in forested streams, agricultural streams tended to be less retentive of organic carbon. These systems function predominantly as conduits transporting organic carbon to downstream

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ecosystems, except during low, stable-flow periods (i.e., late summer) when agricultural streams can be as retentive of organic carbon as forested headwaters. High organic carbon retention in the late summer has implications for coupled carbon and nitrogen cycling (i.e., denitrification), which may play an important role in removing nitrate from stream water during periods of low flow.

Keywords Organic carbon spiraling · Streams · Agriculture · Channelization · Retention · Maize · Filamentous algae · Dissolved organic carbon · Heterotrophic respiration

Introduction

Recent syntheses on the fates of carbon (gas exchange, storage, and transport) have revealed that freshwater ecosystems do not simply act as conduits in transporting carbon to the oceans, but can transform and retain up to half of the carbon that enters from the terrestrial environment (Cole et al. 2007; Battin et al. 2009). Interestingly, small streams were not included in the original analysis by Cole et al. (2007) as there is a lack of global data on outgassing of carbon from these systems. As small streams comprise over two-thirds of the stream length in a typical drainage network (Horton 1945; Leopold et al. 1964; Naiman 1983), there is a need to quantify carbon cycling and fluxes from these ecosystems to more accurately evaluate the role of inland waters in processing and transporting carbon.

The lack of globally-distributed data on carbon fluxes from small streams is a result of most organic carbon budget studies being carried out in relatively pristine, temperate forested environments in the United States (e.g., Fisher and Likens 1973; Wallace et al. 1999; Webster et al. 1999). However, temperate forests make up only a small proportion of all terrestrial landscapes in the world, and even within the United States, most of the land is not forested but rather is used for agricultural rangeland and row crops (Lubowski et al. 2006). Carbon dynamics in streams draining non-forested landscapes may differ from those of forested headwaters that receive substantial quantities of allochthonous detritus (e.g., riparian leaf litter and woody debris) primarily during autumnal leaf fall (Benfield 1997). For example, streams flowing through sagebrush-steppe ecosystems can be fueled almost exclusively by autochthonous (e.g., algae and macrophyte) production (Minshall 1978). Most studies of organic carbon dynamics in open-canopy streams have focused on arid and montane regions in the Western (Minshall 1978; Cushing 1997) and Southwestern U.S. (Fisher et al. 1982; Jones et al. 1997; Dahm et al. 2003; Fellows et al. 2006) and on prairie streams in the Great Plains (Dodds et al. 1996; Gray 1997; Stagliano and Whiles 2002). Relatively little work has been conducted on open-canopied stream ecosystems draining row-crop agriculture (but see Wiley et al. 1990) despite their dominance in the landscape of the Midwestern U.S. (Lubowski et al. 2006).

In the agricultural Midwest, frequent dredging of streams to increase drainage efficiency has decreased channel complexity and removed in-stream structures that retain organic matter. Further, the removal and suppression of riparian zone vegetation and replacement with row crops (e.g., soybeans and maize) has increased light availability and decreased allochthonous carbon inputs to streams, resulting in a dominance of autochthonous production (Wiley et al. 1990). In agricultural streams, the high-light and nutrient-rich environment causes large mats of filamentous green algae (primarily *Cladophora*) to develop in the stream channel (Dodds and Gudder 1992; Winter and Duthie 2000); at times these mats can cover >80% of the stream area during the summer growing season (Schaller et al. 2004). While autochthonous carbon can be the dominant source of organic carbon in agricultural streams, allochthonous material such as grasses and crop detritus may also be important but understudied resources. In the Midwestern U.S., grass buffer strips are planted between the crop field and the stream, and senescent grasses that slump into the stream channel may provide large quantities of allochthonous detritus to aquatic consumers (Menninger and Palmer 2007). Further, in the Midwestern corn belt, maize is a dominant row crop that covered 35.2 million hectares in 2009 (NASS 2009), and after crop harvest, maize leaves, stalks, and cobs are commonly left on fields as a result of conservation tillage and enter streams via wind and surface runoff (Rosi-Marshall et al. 2007). Once in the stream channel, standing stocks of maize detritus can reach

6.4 g ash free dry mass (AFDM)/m^2 (Rosi-Marshall et al. 2007), and leaf detritus decomposes rapidly (Griffiths et al. 2009). We hypothesize that agriculture significantly alters stream organic carbon dynamics by influencing the relative contribution of autochthonous and allochthonous inputs and by changing the retentive capacity of streams, in comparison to well-studied, more pristine forested systems.

In this study, we quantified organic carbon dynamics in agricultural streams using carbon spiraling metrics (Newbold et al. 1982) which integrate measurements of organic carbon pools (in transport and on the benthos), heterotrophic metabolism, and physical parameters (discharge, width, and depth) to describe the fate of organic carbon. Spiraling metrics have been shown to be sensitive to human influences (e.g., Thomas et al. 2005; Taylor et al. 2006) and can be used to compare the relative retentiveness and processing efficiency of organic carbon across streams. The metrics include the organic carbon spiraling length (S_{OC}; km), which is the distance a carbon atom in organic form travels downstream before being respired, and is a function of the velocity at which organic carbon travels downstream (V_{OC}; m/d) and the organic carbon turnover rate (K_{OC}; day^{-1}).

Here, we quantify organic carbon spiraling metrics in 6 agricultural streams during time periods that encompassed maize harvest (autumn and winter) and algal growth (early and late summer) to determine whether the transport and processing of organic carbon changes during these biologically important time periods. We predicted that organic carbon budgets of agricultural streams would be dominated by autochthonous biomass in summer (blooms of filamentous algae, primarily *Cladophora*), and allochthonous inputs (maize detritus) in autumn and winter. We also compare the processing and transport of organic carbon in agricultural streams with published data from less-modified streams (e.g., forested streams). We found that the physical characteristics of agricultural streams in the Midwestern U.S., which include flashy discharge regimes, channelization, and lack of in-stream retention structures, likely caused these streams to act as conduits of organic carbon to downstream ecosystems, with faster downstream velocities of organic carbon (V_{OC}) and longer spiraling lengths (S_{OC}) compared to less-modified (e.g., forested) streams studied in the past (e.g., Minshall et al. 1983; Naiman et al. 1987; Minshall et al. 1992).

Methods

Study sites

We quantified organic carbon spiraling in 6 low-order streams in northwestern Indiana, USA (hereafter designated as streams 2A-F, after Rosi-Marshall et al. 2007). This region is an intensively cultivated area of the Midwestern corn belt, with approximately 97% of land planted in a maize-soybean rotation (NASS 2007). Prior to the conversion to agriculture, historical vegetation surveys and soil maps revealed that streams in this region drained wetlands, tallgrass prairie, and mixed oak and beech-maple forests (Welch 1930; Gordon 1936). The study streams are typical of low-gradient, Midwestern agricultural streams in that they have deeply incised channels, uniform widths, sand/silt-dominated beds with mainly run/pool sequences, and high nitrate concentrations (Table 1) as a result of fertilizer runoff from fields. Riparian zones of these streams consist primarily of grass buffer strips, which vary in lateral distance from crop fields (6–40 m). However, we observed crops planted up to the stream edge along some sections of our study reaches. The study streams are actively managed for effective water drainage and conveyance through frequent dredging and the use of tile drains that underlay fields. As a result of these management practices, stream hydrographs have periods of rapidly changing discharge (i.e., flashy) throughout most of the year (Fig. 1).

We conducted our research during four biologically-important time periods: autumn and winter in 2006 (encompassing crop harvest), and early and late summer in 2007 (encompassing the growth and senescence of filamentous algal blooms, primarily *Cladophora*). We selected 200-m study reaches in 6 low-order streams that were planted with maize on both sides of the stream channel during the 2006 growing season. We sampled 4 streams in autumn (2A, 2B, 2D, 2F) and all 6 streams in winter. We sampled 6 streams in early summer and 4 streams in late summer because streams 2C and 2E were dry at that time of year. During each time period, we sampled one stream per day, thus all streams were completed within a 1–2 week period. Although these streams are hydrologically-variable, we sampled primarily during low-flow periods (Fig. 1), and thus our findings are characteristic of baseflow conditions.

Table 1 Physical and chemical characteristics of 6 agricultural streams in northwestern Indiana, USA measured during 4 biologically important time periods (autumn, winter, early summer, and late summer)

Time period	Sampling Date	Stream	Gradient (m/m)	Mean daily temperature (°C)	Mean discharge (L/s)	Mean velocity (m/s)	Mean width (m)	Mean depth (m)	Mean NO_3^- (mg N/L)	Mean NH_4^+ (μg N/L)	Mean SRP (μg/L)
Autumn	10/14/2006	2A	0.0014	9.07	468	0.35	7.20	0.19	5.2	31.2	7.6
Winter	12/9/2006			3.54	1,120	0.54	7.85	0.28	6.3	22.6	7.5
Early summer	7/8/2007			24.97	232	0.23	7.85	0.13	1.2	<10	5.4
Late summer	9/11/2007			18.65	61	0.13	6.92	0.07	<0.02	12.8	3.2
Autumn	10/8/2006	2B	0.0010	14.44	83	0.27	3.79	0.08	7.7	<10	7.1
Winter	12/10/2006			6.89	153	0.34	4.13	0.11	7.4	11.2	6.6
Early summer	7/7/2007			27.43	12	0.09	2.78	0.05	1.0	22.8	4.3
Late summer	9/16/2007			15.60	1	0.01	2.31	0.02	<0.02	<10	4.3
Winter	12/16/2006	2C	0.0022	6.85	89	0.13	2.91	0.25	8.1	17.0	7.4
Early summer	7/9/2007			28.12	3	0.01	2.58	0.12	0.8	153	6.6
Autumn	10/7/2006	2D	0.0006	14.71	209	0.16	5.78	0.22	6.3	14.6	7.9
Winter	12/15/2006			7.03	797	0.40	8.12	0.24	7.4	15.0	12.4
Early summer	7/11/2007			23.37	80	0.17	4.60	0.10	0.4	<10	2.8
Late summer	9/12/2007			18.47	23	0.07	3.75	0.08	<0.02	<10	3.9
Winter	12/14/2006	2E	0.0029	7.34	57	0.20	1.58	0.19	6.6	12.4	14.7
Early summer	7/12/2007			18.77	5	0.04	1.51	0.08	10.1	<10	6.2
Autumn	10/1/2006	2F	0.0020	17.86	13	0.09	2.97	0.05	8.1	17.2	7.1
Winter	12/8/2006			2.98	113	0.30	3.50	0.11	8.2	26.6	8.6
Early summer	7/13/2007			23.50	6	0.06	2.90	0.04	1.2	29.1	9.0
Late summer	9/17/2007			15.23	1	0.03	2.16	0.01	<0.02	<10	2.3

Mean daily stream water temperature was calculated from measurements taken every 10 min over a 24 h period. Discharge was measured at the top and bottom of the study reach on each sampling date, and width was measured every 5 m along the 200-m study reach. Samples for nitrate (NO_3^-–N), ammonium (NH_4^+–N), and soluble reactive phosphorus (SRP) analysis were collected at the top and bottom of the study reach during each sampling period. The detection limits are 20 μg/L for NO_3^-–N, 10 μg/L for NH_4^+–N and 2 μg/L for SRP

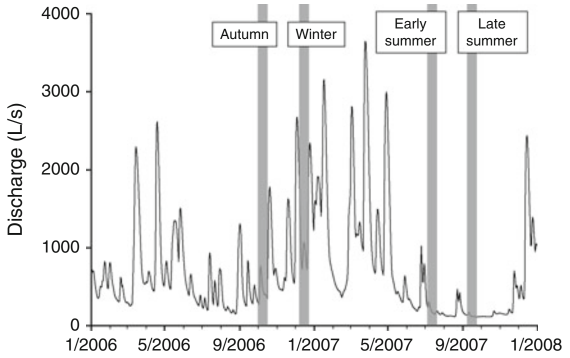


Fig. 1 Discharge from stream 2A in northwestern Indiana, USA from January 1, 2006 to January 1, 2008. Sampling dates (representing the span during which sampling took place) are highlighted in grey. A linear relationship between 2A discharge and discharge from a nearby United States Geological Survey gauge on the Iroquois River in Iroquois, Illinois, USA ($y = 0.0298x + 81.115$, $n = 19$, $r^2 = 0.79$, $P < 0.0001$) was used to interpolate missing data

Field measurements

Transported organic carbon

Total transported organic carbon (TOC) is defined as the sum of coarse particulate (>1 mm, CPOC), fine particulate (52 µm–1 mm, FPOC), and dissolved (<0.7 µm, DOC) organic carbon. In each stream, we collected TOC samples 4 times over a 12-h period, at both an upstream (0 m) and downstream (200 m) station to account for spatial and temporal variability in concentrations of transported organic carbon. We quantified CPOC and FPOC by collecting all material caught in coarse (250-µm) and fine mesh (52-µm) nets that were suspended in the water column for a defined period of time ($\sim$1–2 h for CPOC, and $\sim$5 min for FPOC). We closely monitored the fine-mesh nets for clogging and did not observe any feedback or changes in flow during our $\sim$5 min deployments. To calculate the concentration of organic carbon collected, we determined the volume of water that passed through the nets by measuring depth and water velocity using a velocity meter (Flo-Mate, Model 2000 Portable Flowmeter, Marsh-McBirney Inc/Hach Flow, Loveland, Colorado, USA) at 3 locations across the known width of the net. We then washed organic matter trapped in the nets into 120-mL specimen cups and froze them at −30°C until laboratory analysis. In the laboratory, we washed each CPOC sample into a 1-mm sieve, placed caught material in a pre-weighed aluminum pan, and qualitatively identified the organic matter (maize, filamentous algae, grass fragments, deciduous leaves, invertebrates). We passed FPOC samples through a 1-mm sieve and collected the filtrate on an ashed, pre-weighed glass-fiber filter (GF/F, Whatman Inc., Florham Park, New Jersey, USA). We then dried the CPOC and FPOC samples in a drying oven at 60°C for 48 h, and combusted them in a muffle furnace at 550°C for 2 h. We quantified ash-free dry mass (AFDM) as the difference between ash and dry masses, and AFDM was converted to organic carbon using a 48.4% organic carbon:AFDM conversion factor (Thomas et al. 2005). We measured dissolved organic carbon (DOC) on a Shimadzu TOC-CPN analyzer from a filtered (0.7 µm, GF/F, Whatman Inc.), acidified (pH 2) water sample collected simultaneously with each CPOC and FPOC sample.

Benthic organic carbon

We quantified total benthic organic carbon (BOC) using the habitat-weighted transect approach (Hoellein et al. 2007). Because BOC collection disturbs the benthos, we sampled benthic organic matter 1–2 days after TOC and organic carbon turnover sampling (described below). We marked 21 transects spaced 10 m apart along each 200-m reach. At every 20-cm interval across each transect we recorded the substratum type and water depth. We later classified substrata into fine (accumulations of fine organic particles, and fine organics on sand, gravel, and cobble) and coarse (maize detritus, filamentous algae, grass, macrophyte, and bryophyte) particulate organic matter categories. We then sampled the standing stocks of the dominant substrata in each stream by placing a subsampler with a known area (28, 79, or 314-cm^2 depending on the substratum sampled) over a region of the benthos that was covered at 100% by the particular substratum ($n = 5$ samples per substratum type). We collected all material within the subsampler, measured AFDM, and converted to carbon as described above. We then scaled the organic carbon content of each substratum to the entire stream reach (units: g C/m^2 stream bottom) based on its proportional abundance determined from the transects.

Organic carbon turnover rates

We quantified turnover rates of organic carbon using two approaches: (1) the open-water exchange method of measuring whole-stream metabolism (Odum 1956; Bott 2006), and (2) substrate-specific heterotrophic respiration on accumulations of fine organic particles (Hill et al. 1998, 2000). We employed both of these approaches in our study design as they quantify heterotrophic respiration at different spatial and temporal scales, and with different respective advantages and caveats (see Young et al. 2008; Tank et al. 2010 for discussion). We measured whole-stream metabolism using the one-station, open-water exchange method (Odum 1956; Bott 2006) where we placed a field-calibrated data-logging sonde (Hydrolab Minisonde 4a, Hach Company, Loveland, Colorado, USA) at the bottom of the study reach, and logged dissolved oxygen concentration and water temperature every 10 min for 36 h. We also measured photosynthetically active radiation (PAR) every 10 min over the same time period using a logging light meter (Odyssey Photosynthetic Irradiance Recording System, Dataflow Systems PTY Ltd, Christchurch, New Zealand), which we placed beside the sonde at 10 cm above the water surface. We collected all data during baseflow and on clear, sunny days, usually 1–2 days prior to TOC sampling. Gross primary production (GPP), ecosystem respiration (ER), and the reaeration coefficient of oxygen (K) were estimated using the day-time regression model (Kosinski 1984) using ModelMaker 4.0 (AP Benson, Wallingford, United Kingdom) (see Atkinson et al. 2008 for explanation of the model). As ER does not partition autotrophic and heterotrophic respiration, and carbon spiraling metrics require partitioning respiration by heterotrophs, we converted ER to heterotrophic respiration (R_{het}) rates by assuming that 20% of GPP is respired by autotrophs (McIntire et al. 1996; Young and Huryn 1999). We then converted heterotrophic respiration rates from g O_2 m^{-2} day^{-1} to g C m^{-2} day^{-1} using a respiratory quotient of 0.85 and the molar ratio of atomic C to O_2 (Bott 2006).

We measured substrate-specific R_{het} on accumulations of fine organic particles collected along each 200-m reach. We selected fine organics because they are the dominant benthic substrate in these systems and have been shown to be a hot-spot for heterotrophic respiration (Hoellein et al. 2009). We collected one fine organics sample every 5 m ($n = 40$) by placing an inverted 60-mL centrifuge tube 1 cm into benthos and capping the bottom to remove. We returned the samples to the laboratory, stored them overnight at 4°C, and analyzed them for microbial respiration the following day. First, we decanted the stream water overlying the samples and re-filled each centrifuge tube with filtered stream water (GF/F) being careful to eliminate any air bubbles. We quantified microbial respiration on fine organic particles (expressed in g C m^{-2} day^{-1} and converted from O_2 as described above) by measuring the change in dissolved oxygen concentration over a 2-h incubation period (in the dark) using a hand-held dissolved oxygen probe (DO200, Yellow Springs Instruments, Inc., Yellow Springs, Ohio, USA) (Hill et al. 1998, 2000). To compare substrate-specific heterotrophic metabolism rates to whole-stream respiration rates, we incubated samples at temperatures encompassing the lowest and highest temperatures recorded on the sampling date in each stream (autumn: 10–20°C; winter: 2.5–20°C; early summer: 20–35°C; late summer: 12–20°C). We included tubes containing only stream water as blanks ($n = 5$ per stream) to account for any changes in dissolved oxygen attributed to the water column alone.

Physical and chemical parameters

We measured stream velocity using a velocity meter at the top and bottom of each reach and calculated discharge (Q) using the velocity-area protocol (Gore 2006). To calculate mean stream width (w), we averaged widths measured from 41 evenly-spaced (every 5 m) transects. To measure mean water velocity (V_{water}), we released a concentrated salt (NaCl) slug at the top of the study reach, and measured the time it took for conductivity to peak 200 m downstream of the release point. We then calculated mean stream depth (z) based on continuity ($Q = V_{water} \bullet z \bullet w$). To measure stream water nutrient concentrations, we collected water samples at the upstream and downstream stations at the end of the TOC sampling period. We filtered water samples (GF/F) into acid-washed, polypropylene bottles, and froze the samples at −30°C until analysis. We measured nitrate–N concentrations using the cadmium reduction method (APHA 1995), ammonium–N concentrations using the phenol-hypochlorite method (Solorzano 1969), and soluble reactive phosphorus (SRP) concentrations using the molybdateantimony method (Murphy and Riley 1962) on a Lachat QC8500 Flow Injection Autoanalyzer (Lachat Instruments, Loveland, Colorado, USA).

Carbon spiraling metrics

We calculated organic carbon spiraling metrics using the TOC, BOC, organic carbon turnover, and physical parameters described above. Specifically, we calculated the downstream velocity of organic carbon (V_{OC}; m/d), the organic carbon turnover rate (K_{OC}; day^{-1}), and the organic carbon spiraling length (S_{OC}; km). Further, we assessed the retentive capacity of streams using the index of retention (IR; Minshall et al. 1992) which equals the ratio of water velocity (V_{water}; m/d) to the downstream velocity of organic carbon (V_{OC}), with streams with a ratio approaching 1 acting as conduits for downstream organic carbon transport, and streams with a ratio >1 being more retentive of organic carbon. The equations for these four metrics which were derived by Newbold et al. (1982) and Minshall et al. (1992) are shown below:

$$V_{OC} = \frac{TOC \times Q}{BOC \times w} \quad (1)$$

$$K_{OC} = \frac{R_{het}}{BOC + (TOC \times z)} \quad (2)$$

$$S_{OC} = \frac{V_{OC}}{K_{OC}} \quad (3)$$

$$IR = \frac{V_{water}}{V_{OC}} \quad (4)$$

where TOC = total transported organic carbon concentration (g/m^3), Q = discharge (m^3/d), BOC = total benthic organic carbon standing stock (g/m^2), w = mean stream width (m), R_{het} = heterotrophic respiration (g C m^{-2} day^{-1}), and z = mean stream depth (m).

Statistical analyses

We examined seasonal differences in carbon spiraling metrics (S_{OC}, V_{OC}, K_{OC}, and IR) and associated parameters (e.g., TOC, BOC, R_{het}) using one-way analysis of variance (ANOVA) blocked by stream. If the main effect (season) was significant ($P < \alpha = 0.05$), we used a Tukey's Honestly Significant Difference post-hoc test to determine which sample periods were statistically different from each other. We reported the effect of the block (i.e., stream) to examine whether significant differences existed among streams, but the block effect was not examined further using post-hoc tests. We note that while we attempted to quantify seasonality in carbon spiraling metrics, we recognize that any seasonal patterns likely reflect both seasonal changes through time as well as differences in hydrology.

We used backward stepwise multiple linear regression ($P = 0.15$ to remove a variable) to examine which parameters (stream water nutrient concentrations, water temperature, benthic organic carbon standing stocks) influenced heterotrophic respiration. We used correlation analysis to identify which parameter(s) in each of the carbon spiraling equations explained the variation in spiraling metrics. We recognize that some parameter(s) in each of the carbon spiraling equations will be inherently correlated with the spiraling metrics themselves, and thus we are using the correlation analyses to partition out the variation in each carbon spiraling metric among the parameters from which each metric was calculated. For example, the variation in S_{OC} may be assumed to be driven by variation in V_{OC} but not K_{OC} due to a significant correlation between S_{OC} and V_{OC}, and a non-significant correlation between S_{OC} and K_{OC} (see Eq. 3).

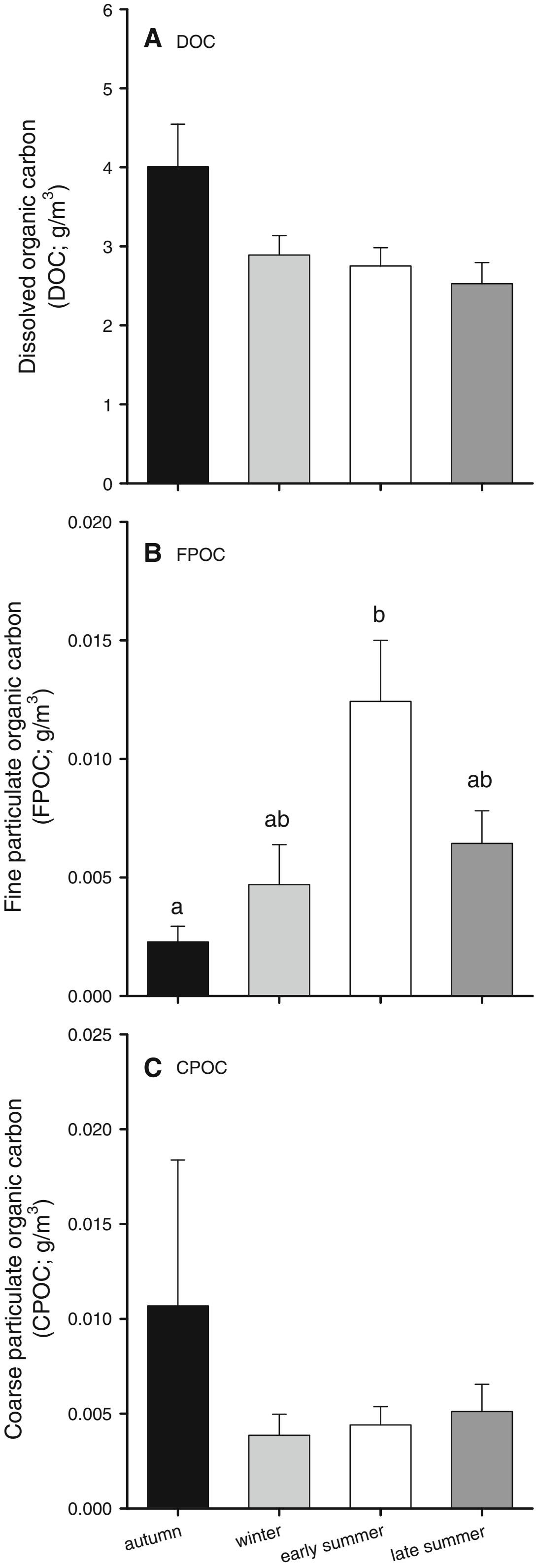
To compare organic carbon spiraling metrics in agricultural streams to previously published data, we compared the slopes of the two regression lines of the S_{OC} versus discharge relationships using an analysis of covariance (ANCOVA) that examined the interaction between stream type (agricultural streams vs. previously published data) and stream discharge. When necessary, we normalized data to meet parametric assumptions using natural log transformations, and all statistical analyses were performed using SYSTAT 12.0 (SYSTAT 2007).

Results

Components of transported organic carbon

In general, there were no significant differences among streams for concentrations of all three transported forms of organic carbon; however, there were significant differences in dissolved organic carbon (DOC) and fine particulate organic carbon (FPOC) concentrations among seasons. DOC concentrations ranged

Fig. 2 Transported organic carbon as: **(a)** dissolved organic carbon (DOC; g/m^3), **(b)** fine particulate organic carbon (FPOC; g/m^3), and **(c)** coarse particulate organic carbon (CPOC; g/m^3) (mean ± standard error) for each biologically important time period (autumn, winter, early summer, and late summer). Error reflects variation among streams ($n = 6$ for winter and early summer; $n = 4$ for autumn and late summer). *Letters* represent significant differences between seasons based on results from Tukey's HSD post-hoc tests



from 1.97 to 5.62 g/m^3, and dominated the budget of total transported organic carbon (TOC) by accounting for over 99% of TOC in all streams and seasons. There were seasonal differences in DOC concentration (Fig. 2a, one-way ANOVA, $P = 0.049$), with DOC being slightly higher in autumn than in early (Tukey's HSD, $P = 0.07$) and late summer (Tukey's HSD, $P = 0.06$). However, these differences were mainly driven by higher DOC concentrations in stream 2F in autumn (5.62 g/m^3). DOC loads ranged from 0.16 to 2,475.43 kg/d and differed among seasons (one-way ANOVA, $P < 0.0001$) with the largest loads in winter and the smallest loads in late summer (Tukey's HSD, $P < 0.0001$). There were significant differences in DOC loads among streams (one-way ANOVA, $P < 0.0001$), with the larger streams (2A, 2D) having larger loads than the smaller streams (2B, 2C, 2E, 2F).

Transported FPOC made up only 0.02 to 0.67% of the TOC budget, although concentrations differed significantly among seasons (Fig. 2b, one-way ANOVA, $P = 0.03$), with FPOC being significantly higher in early summer than in autumn (Tukey's HSD, $P = 0.04$). Transported FPOC loads ranged from 0.55 to 1,121.47 g/d, with significant seasonal patterns (one-way ANOVA, $P < 0.0001$) of the largest loads in winter and the smallest loads in late summer (Tukey's HSD, $P < 0.0001$). Similar to DOC loads, there were significant differences in FPOC loads among streams (one-way ANOVA, $P < 0.0001$), with larger streams carrying larger loads than smaller streams.

Transported coarse particulate organic carbon (CPOC) comprised 0.004 to 0.6% of the TOC budget, and did not differ among seasons (Fig. 2c, one-way ANOVA $P = 0.83$). Transported CPOC loads ranged from 0.48 to 529.15 g/d, with significant seasonal patterns (one-way ANOVA, $P = 0.0002$) of larger CPOC loads in winter than in late summer (Tukey's HSD, $P = 0.0002$). Further, there were significant differences in CPOC loads among streams (one-way ANOVA, $P = 0.001$), with the larger streams tending to have larger CPOC loads than the smaller streams. Most of the CPOC samples were composed of filamentous algae, deciduous leaves, grass fragments, and invertebrates. Identifiable maize detritus was only found in autumn in one stream (2E), and at that time it comprised 10% of the CPOC budget. Similar to DOC, the highest CPOC concentrations were measured in stream 2F in autumn, and these samples mainly contained filamentous algae (*Cladophora*) that had presumably sloughed off senescent mats.

Components of benthic organic carbon

Benthic organic carbon standing stocks ranged from 41 to 241 g/m^2, and there were significant differences in BOC, CBOC, and FBOC among streams, but not among seasons. Specifically, BOC did not differ by season (one-way ANOVA, $P = 0.53$), and was significantly different among streams (one-way ANOVA, $P = 0.0008$) with streams 2A, 2E, and 2F generally having smaller BOC standing stocks than streams 2B, 2C, and 2D. In examining the components of BOC, coarse benthic organic carbon (CBOC) (maize detritus, filamentous algae, grass, macrophytes, bryophytes) differed by stream (one-way ANOVA, $P = 0.03$), primarily due to the dominance of grass in stream 2B, which comprised 81–100% of the CBOC pool across all seasons. There were no significant differences in CBOC among seasons (Fig. 3a, one-way ANOVA, $P = 0.16$), but CBOC tended to be lowest in early summer. In early summer, filamentous algae comprised over 80% of the CBOC pool in half of the streams, while algae only comprised 3–18% of the CBOC pool in late summer. In the winter, benthic detritus consisting of maize was found in only one stream (2C) and comprised 1% of the CBOC pool. Maize detritus was also present in late summer, and made up 0.2, and 4.9% of the CBOC pool in streams 2A and 2D, respectively.

There were no differences in fine benthic organic carbon (FBOC) (accumulations of fine organic particles, and fine organics on sand, gravel, and cobble) among seasons (Fig. 3b, one-way ANOVA, $P = 0.35$), but FBOC differed among streams (one-way ANOVA, $P = 0.004$). The dominant component of the benthos in these agricultural streams was either accumulations of fine organic particles or sand (and associated fine organic particles). As such, some streams were dominated by fine organics (up to 100% of the FBOC pool) and others by sand with fine organics (up to 95% of the FBOC pool). Interestingly, streams with a benthos dominated by fine organic particles in one season sometimes switched to being predominantly sand in another season, emphasizing the transient and movable nature of the benthic

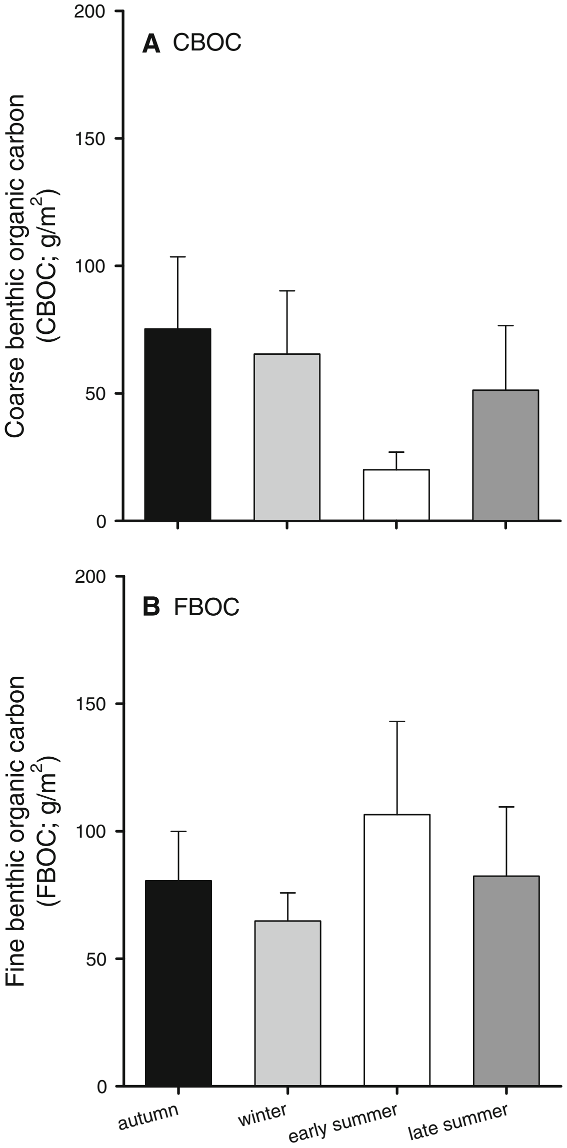


Fig. 3 Benthic organic carbon as: (**a**) coarse benthic organic carbon (CBOC; g/m^2) and (**b**) fine benthic organic carbon (FBOC; g/m^2) standing stocks (mean ± standard error) for each biologically important time period (autumn, winter, early summer, and late summer). Error reflects variation among streams ($n = 6$ for autumn, winter, and early summer; $n = 4$ for late summer)

sediments in agricultural streams; however, this pattern was not predictable among seasons or streams.

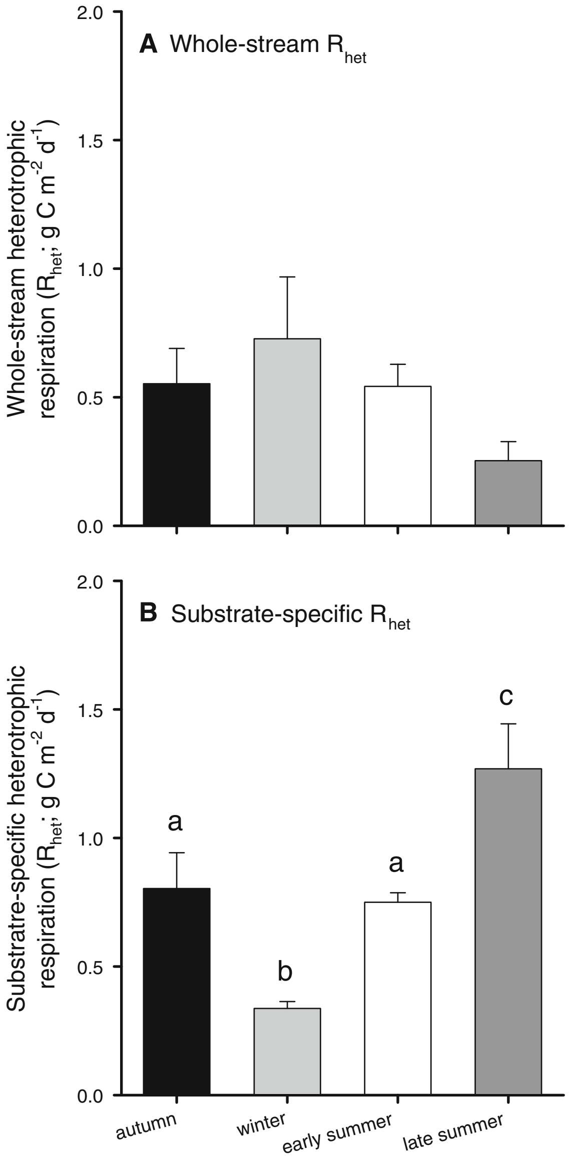


Fig. 4 Heterotrophic respiration (R_{het}) as: (**a**) whole-stream respiration rates (g C m^{-2} day^{-1}) and (**b**) substrate-specific respiration rates (g C m^{-2} day^{-1}) on accumulations of fine organic particles incubated at 20°C (mean ± standard error) for each biologically important time period (autumn, winter, early summer, and late summer). Error reflects variation among streams ($n = 6$ for winter and early summer; $n = 4$ for autumn and late summer). *Letters* represent significant differences between seasons based on results from Tukey's HSD post-hoc tests

Organic carbon turnover: R_{het} via whole-stream and substrate-specific measurements

Seasonal patterns in heterotrophic respiration (R_{het}) depended on whether we used whole-stream or substrate-specific respiration. Whole-stream R_{het} did not differ among seasons (Fig. 4a, one-way ANOVA, $P = 0.42$), but tended to be highest in winter and lowest in late summer. Whole-stream R_{het} also did not differ among streams (one-way ANOVA, $P = 0.08$), but stream 2E had a much higher R_{het} in winter compared to any other stream and on any other date. Further, R_{het} was positively related to SRP concentration (stepwise multiple linear regression, $r^2 = 0.39$, $P = 0.003$) but not benthic organic carbon standing stocks, stream water temperature, nitrate, or ammonium concentrations. In contrast, substrate-specific R_{het} differed among seasons (Fig. 4b, one-way ANOVA, $P = 0.0002$), and showed an opposite trend to whole-stream R_{het} with the lowest rates in winter and the highest rates in late summer (Tukey's HSD, $P = 0.0001$). However, similar to whole-stream R_{het}, there were no significant differences among streams in substrate-specific R_{het} (one-way ANOVA, $P = 0.23$). Further, substrate-specific R_{het} was positively related to stream water temperature (stepwise multiple linear regression, $r^2 = 0.48$, $P = 0.0007$), but not benthic organic carbon standing stocks, nitrate, ammonium, or SRP concentrations.

Carbon spiraling metrics

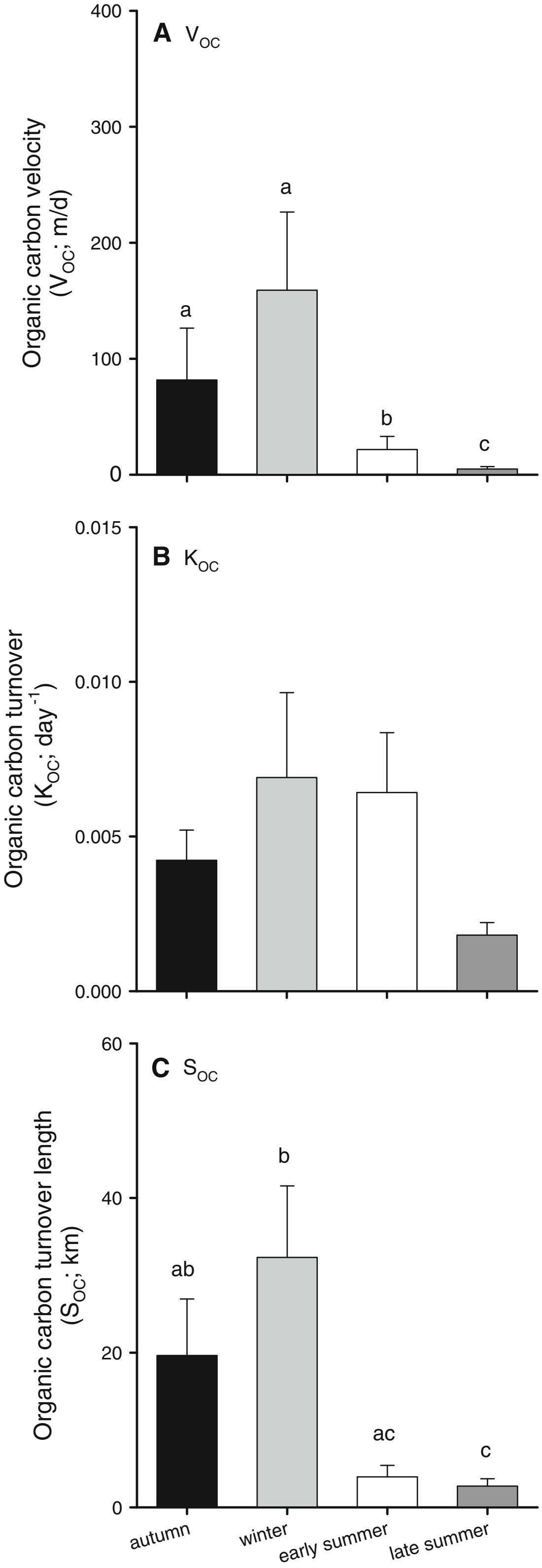
The downstream velocity of organic carbon (V_{OC}) varied by almost 3 orders of magnitude from 1 m/d in stream 2B in late summer to 483 m/d in stream 2A in winter (Table 2), and was significantly different among streams (one-way ANOVA, $P = 0.0006$) and seasons (Fig. 5a, one-way ANOVA, $P < 0.0001$). Specifically, V_{OC} was faster in the larger stream (2A) compared to the smaller streams (2B, 2C, 2E, 2F). Further, V_{OC} rates were faster in autumn and winter (Tukey's HSD, all $P < 0.05$) and slower in early and late summer (Tukey's HSD, all $P < 0.05$). Using correlation analysis, we examined the four components of the V_{OC} equation (TOC, Q, BOC, w) and their influence on V_{OC}. Only discharge (Q) and secondarily stream width (w) were significantly, positively correlated with V_{OC} (Q: $R = 0.91$, $P < 0.0001$, w: $R = 0.52$, $P = 0.018$). However, if stream width was

Table 2 Mean carbon spiraling metrics measured in 6 agricultural streams in northwestern Indiana, USA during 4 biologically important time periods (autumn, winter, early summer, and late summer)

Time period	Stream	DOC (g/m^3)	FPOC (g/m^3)	CPOC (g/m^3)	TOC (g/m^3)	FBOC (g/m^2)	CBOC (g/m^2)	BOC (g/m^2)	Substrate R_{het}, low T (g C m^{-2} day^{-1})	Substrate R_{het}, high T (g C m^{-2} day^{-1})	Whole-stream R_{het} (g C m^{-2} day^{-1})	V_{OC} (m/d)	K_{OC} (day^{-1})	S_{OC} (km)	IR
Autumn	2A	3.57	0.002	0.004	3.57	92	2	94	0.58	0.65	0.54	215	0.0057	37.5	145
	2B	3.45	0.002	0.004	3.46	50	108	158	0.71	1.22	0.26	41	0.0017	25.0	583
	2D	3.38	0.001	0.002	3.39	98	143	241	0.48	0.67	0.92	44	0.0038	11.5	323
	2F	5.62	0.004	0.034	5.66	76	8	84	0.59	0.67	0.48	26	0.0057	4.6	307
Winter	2A	2.51	0.012	0.005	2.53	58	6	64	0.28	0.32	0.58	483	0.0090	53.8	98
	2B	2.21	0.003	0.007	2.22	41	174	215	0.28	0.25	0.30	33	0.0014	23.4	952
	2C	2.81	0.001	0.001	2.82	74	72	146	0.29	0.27	0.98	51	0.0067	7.7	223
	2D	3.59	0.008	0.006	3.61	115	82	197	0.32	0.39	0.57	156	0.0029	54.4	232
	2E	3.66	0.003	<0.001	3.66	47	44	92	0.23	0.39	1.78	125	0.0193	6.5	137
	2F	2.55	0.002	0.003	2.56	52	15	68	0.40	0.41	0.15	106	0.0022	48.3	254
Early summer	2A	2.32	0.005	0.002	2.33	71	6	77	0.79	0.91	0.77	77	0.0099	7.8	265
	2B	2.52	0.016	0.008	2.54	95	43	138	0.86	1.24	0.26	7	0.0019	3.7	1,172
	2C	3.16	0.021	0.005	3.18	222	1	223	0.69	0.76	0.81	1	0.0036	0.4	664
	2D	2.36	0.012	0.003	2.37	210	12	222	0.64	0.66	0.40	16	0.0018	9.0	906
	2E	2.43	0.005	0.005	2.44	18	23	41	0.68	0.87	0.54	16	0.0133	1.2	222
	2F	3.72	0.014	0.004	3.74	23	36	59	0.84	0.92	0.47	12	0.0080	1.5	447
Late summer	2A	1.97	0.004	0.001	1.98	111	16	127	0.95	1.39	0.33	12	0.0026	4.5	1,008
	2B	3.44	0.009	0.008	3.45	21	126	148	1.26	1.69	0.39	1	0.0027	0.2	2,267
	2D	2.14	0.003	0.003	2.15	142	33	175	0.59	0.89	0.23	7	0.0013	5.0	1,110
	2F	2.55	0.010	0.008	2.57	55	30	85	0.77	1.10	0.06	1	0.0007	1.3	2,912

DOC dissolved organic carbon concentration, *FPOC* fine particulate organic carbon concentration, *CPOC* coarse particulate organic carbon concentration, *TOC* total transported organic carbon concentration, *FBOC* fine benthic organic carbon standing stock, *CBOC* coarse benthic organic carbon standing stock, *BOC* benthic organic carbon standing stock, *substrate-specific* R_{het} heterotrophic respiration measured on fine organic particles at the low incubation temperature (low T; 2.5–20°C, depending on stream and season) and high incubation temperature (high T; 20–35°C, depending on stream and season), *whole-stream* R_{het} heterotrophic respiration measured for the whole stream, V_{OC} downstream velocity of organic carbon, K_{OC} organic carbon turnover rate, S_{OC} organic carbon turnover length, and *IR* index of retention of organic carbon

Fig. 5 Organic carbon spiraling metrics: (**a**) organic carbon ▶ velocity (V_{OC}; m/d), (**b**) biotic turnover rate of organic carbon (K_{OC}; day^{-1}), and (**c**) organic carbon turnover length (S_{OC}; km) (mean ± standard error) for each biologically important time period (autumn, winter, early summer, and late summer). Error reflects variation among streams ($n = 6$ for winter and early summer; $n = 4$ for autumn and late summer). *Letters* represent significant differences between seasons based on results from Tukey's HSD post-hoc tests



influencing V_{OC}, we would expect a negative correlation between stream width and V_{OC} as stream width is in the denominator of the V_{OC} equation. Thus, the variation in V_{OC} is primarily driven by variation in Q, and the correlation with stream width instead reflects the correlation of Q and w (higher discharge, wider streams). There were no significant correlations between V_{OC} and TOC ($R = 0.08$, $P = 0.74$) or BOC ($R = 0.21$, $P = 0.39$).

The turnover rate of organic carbon (K_{OC}) varied almost two orders of magnitude from 0.0007 day^{-1} in stream 2F in late summer to 0.0193 day^{-1} in stream 2E in winter (Table 2), and K_{OC} varied among streams (one-way ANOVA, $P = 0.001$) but not seasons (Fig. 5b, one-way ANOVA, $P = 0.36$). The among-stream differences appear to be driven by faster turnover rates in stream 2E compared to all other streams (Table 2). Variation in K_{OC} was driven both by R_{het} and BOC as there was a significant, positive correlation between K_{OC} and R_{het} ($R = 0.81$, $P < 0.0001$) and a significant, negative correlation between K_{OC} and BOC ($R = 0.52$, $P = 0.02$). There was also a significant, positive correlation with K_{OC} and stream depth (z) ($R = 0.46$, $P = 0.04$), although as with V_{OC} and w, not in the predicted direction. There was no significant correlation between K_{OC} and TOC ($R = 0.26$, $P = 0.28$).

Organic carbon spiraling length (S_{OC}) varied by over two orders of magnitude, ranging from 0.2 km in stream 2B in late summer to 54.4 km in stream 2D in winter (Table 2), and was significantly different among streams (one-way ANOVA, $P = 0.02$) and seasons (Fig. 5c, one-way ANOVA, $P = 0.0003$). Specifically, the shortest spiraling lengths were measured primarily in streams 2C and 2E (means across seasons were 4.0 km for 2C and 3.8 km for 2E), the longest spiraling lengths found in streams 2A and 2D (means across seasons were 25.9 km for 2A and 20.0 km for 2D), and intermediate spiraling lengths in streams 2B and 2F (means across seasons were

13.1 km for 2B and 13.9 km for 2F) (Table 2). Further, the longest spiraling lengths occurred in winter and the shortest were measured in early (Tukey's HSD, $P = 0.002$) and late summer (Tukey's HSD, $P = 0.0005$). There was a significant, positive correlation between V_{OC} and S_{OC} ($R = 0.87$, $P < 0.0001$) but not K_{OC} and S_{OC} ($R = 0.005$, $P = 0.98$), suggesting that seasonal and among-stream variation in S_{OC} is driven by variation in V_{OC}.

The index of retention (IR) varied 30-fold, from 98 in stream 2A in winter to 2,912 in stream 2F in late summer (Table 2), and was significantly different among seasons (one-way ANOVA, $P = 0.002$) but not streams (one-way ANOVA, $P = 0.13$). While IR did not differ among streams, the largest stream (2A) tended to be the least retentive in all seasons. Further, streams in late summer were the most retentive (highest IR) compared to all other time periods (Tukey's HSD, all $P < 0.05$). Variation in IR was driven by V_{OC} ($R = 0.87$, $P < 0.0001$) and V_{water} ($R = 0.59$, $P = 0.006$). However, the significant correlation between IR and V_{water} was probably due to the overwhelming influence of discharge (as part of the V_{OC} equation) on IR ($R = 0.67$, $P = 0.001$). No other components of the V_{OC} equation were significantly correlated with IR (TOC: $R = 0.24$, $P = 0.30$; w: $R = 0.26$, $P = 0.28$; BOC: $R = 0.31$, $P = 0.09$).

Influence of R_{het} from whole-stream vs. substrate-specific methods on carbon spiraling metrics

Because the two methods we used to estimate R_{het} yielded contrasting seasonal patterns, we examined how these differences impacted carbon spiraling metrics, namely K_{OC} and S_{OC}. We calculated K_{OC} and S_{OC} using R_{het} determined from the substrate-specific method at both the low and high incubation temperatures, and compared these metrics to K_{OC} and S_{OC} calculated from whole-stream R_{het}. Because K_{OC} is directly proportional to S_{OC}, only changes in S_{OC} are shown in Table 3. S_{OC} lengths tended to be similar when calculated from the substrate-specific R_{het} incubated at low vs. high temperatures (Table 3). In contrast, using whole-stream R_{het} vs. substrate-specific R_{het} strongly influenced estimates of S_{OC}. For example, using substrate-specific R_{het} in carbon spiraling calculations measured in winter tended to increase S_{OC} in almost all streams relative to S_{OC} calculated with whole-stream R_{het} (Table 3), with the greatest increase in S_{OC} in stream 2E being almost an order of magnitude, from 6.5 to 49.4 km. In contrast, using substrate-specific R_{het} in carbon spiraling calculations measured in late summer tended to decrease S_{OC} in all streams relative to S_{OC} calculated with whole-stream R_{het} (Table 3), with the largest decrease in stream 2F being over an order of magnitude from 1.3 to 0.07 km. Despite these changes in S_{OC} (through changes in K_{OC}), we determined that when we used different R_{het} methodologies, the same seasonal patterns in S_{OC}

Table 3 Comparison of S_{OC} (km) calculated using 2 different R_{het} methods: whole-stream R_{het} and substrate-specific R_{het} at low and high incubation temperatures

Time period	Stream	Substrate-specific R_{het} (low T): whole-stream R_{het}	Substrate-specific R_{het} (high T): whole-stream R_{het}	Substrate-specific R_{het} (low T): substrate-specific R_{het} (high T)
Autumn	2A	0.9	0.8	1.1
	2B	0.4	0.2	1.7
	2D	1.9	1.4	1.4
	2F	0.8	0.7	1.1
Winter	2A	2.1	1.8	1.1
	2B	1.1	1.2	0.9
	2C	3.4	3.7	0.9
	2D	1.8	1.5	1.2
	2E	7.6	4.6	1.7
	2F	0.4	0.4	1.0
Early summer	2A	1.0	0.8	1.2
	2B	0.3	0.2	1.4
	2C	1.2	1.1	1.1
	2D	0.6	0.6	1.0
	2E	0.8	0.6	1.3
	2F	0.6	0.5	1.1
Late summer	2A	0.4	0.2	1.5
	2B	0.3	0.2	1.3
	2D	0.4	0.3	1.5
	2F	0.1	0.1	1.4

For the first two data columns, a ratio greater than one indicates that substrate-specific R_{het} method resulted in longer S_{OC}, while a ratio less than one indicates that the substrate-specific method resulted in shorter S_{OC}. Using substrate-specific R_{het} in carbon spiraling calculations tended to increase S_{OC} in almost all streams in winter relative to S_{OC} calculated with whole-stream R_{het}. In contrast, using substrate-specific R_{het} in carbon spiraling calculations tended to decrease S_{OC} in all streams in late summer relative to S_{OC} calculated with whole-stream R_{het}

(longest S_{OC} in winter and shortest S_{OC} in late summer) emerged, most likely due to the overwhelming dominance of V_{OC} (via discharge) on estimates of S_{OC}.

Discussion

Organic carbon dynamics in these agricultural streams were strongly driven by variation in discharge, and we suggest that the altered hydrology of agricultural streams (i.e., channelization and sub-surface tile drainage) causes these streams to act as conduits for the downstream transport of organic carbon. We support this finding by comparing the efficiency of carbon utilization (S_{OC}) in these agricultural streams with published data primarily from less-modified streams. Specifically, we compared S_{OC} to streams of similar size by building upon the regression of discharge vs. S_{OC} that was originally developed by Young and Huryn (1999) (Fig. 6). The S_{OC} and discharge data included in this regression are dominated by less-modified streams, such as Kings Creek in Konza Prairie, Kansas (Gray 1997), Walker Branch, Tennessee (Mulholland 1997b), and Sycamore Creek, Arizona (Jones et al. 1997), but include some data from more human-altered streams, such as developed pasture and exotic pine plantations along tributaries of the Taieri River in New Zealand (Young and Huryn 1999) and the mixed agricultural-municipal watershed of the Middle Snake River in Idaho (Thomas et al. 2005). Agricultural streams from this study draining intensive row-crop agriculture fall within the relationship of previously published data; however, the slope of the S_{OC} versus discharge relationship was steeper for these agricultural streams (slope = 0.68) compared to the other studies (Fig. 6, ANCOVA, slope = 0.39, $P = 0.04$). These results suggest that at higher discharges, channelized agricultural streams may be acting more like conduits for the downstream transport of organic carbon compared to more retentive reference systems.

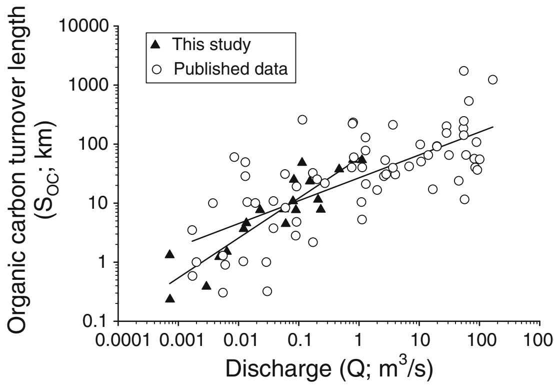


Fig. 6 Relationships between discharge (Q; m^3/s) and organic carbon turnover length (S_{OC}; km) from this study (*black triangles*; $y = 0.68x + 1.76$, $n = 20$, $r^2 = 0.83$, $P < 0.0001$) and from previously published studies (*white circles*; $y = 0.39x + 1.43$, $n = 68$, $r^2 = 0.50$, $P < 0.0001$). Previously reported data are from Minshall et al. (1983, 1992), Thomas et al. (2005), Webster and Meyer (1997), and Young and Huryn (1997, 1999)

Components of transported organic carbon

DOC concentrations measured at baseflow dominated carbon flux by comprising over 99% of transported organic carbon, and were similar among seasons and streams, ranging from 1.97 to 5.62 g/m^3. Baseflow DOC concentrations in agricultural streams generally range from 1 to 8 mg/L (equivalent to g/m^3) (Dalzell et al. 2005, 2007; Royer and David 2005; Vidon et al. 2008; Warrner et al. 2009; this study); in comparison, dissolved organic matter concentrations in less-disturbed streams across North America range from 1 to >35 mg/L (Mulholland 1997a). Agricultural soils are the primary source of DOC to streams, and lower DOC concentrations are attributed to the reduced organic carbon content of agricultural soils as a result of cultivation practices (Cronan et al. 1999). Despite these lower DOC concentrations, DOC is the dominant component of organic carbon exported from these agricultural watersheds. The highest DOC concentration was measured in stream 2F in autumn, and this was the only stream at that time that had a large filamentous algal bloom comprising 69% of the coarse benthic organic carbon pool. Algal production can provide an autochthonous source of labile DOC to streams (Kaplan and Bott 1982) and may have contributed to the higher concentration of DOC we measured in autumn. However, a more detailed analysis of DOC dynamics in these streams during the summer algal bloom revealed that there were no increases in DOC concentration or bioavailability in the day vs. night, possibly because labile autochthonous DOC is respired rapidly (Warrner et al. 2009).

Transported fine particulate organic carbon (FPOC) made up a small proportion of the total organic carbon in transport (0.02 to 0.67%), and FPOC concentrations were highest in early summer when algal blooms dominated the benthos. In early summer, there was a positive, but marginally-significant correlation between FPOC concentrations in the water column and the FBOC standing stocks in the 6 study streams ($R = 0.74$, $P = 0.09$), suggesting that the benthos could be a local source and/or sink of organic particles in the water column. The sources of FPOC were not identified in this study, but may have included the decomposition byproducts of organic detritus (Suberkropp and Klug 1980; Ward 1984), including maize and filamentous algae, maize pollen that blew in during summer pollen shed (Rosi-Marshall et al. 2007), aggregation of dissolved organic matter (Petersen 1986), and feces from invertebrates (Wallace and Webster 1996). We did not measure the ultra-fine organic carbon fraction (between DOC and FPOC) in this study, and this missing fraction may have made up a considerable portion of the transported organic carbon (Thomas et al. 2005). However, in Big Pine Creek watershed in northwestern Indiana, the colloidal organic carbon fraction of DOC (0.2–0.7 μm) comprised a small portion of the overall DOC pool (Dalzell et al. 2005). Nevertheless, the missing fraction of ultra-fine organic carbon would most likely not impact the seasonal patterns in spiraling metrics we observed due to the overwhelming influence of discharge on these metrics. Further, we note that we found a strong hydrologic control on organic carbon dynamics despite sampling primarily during baseflow conditions.

There were no seasonal patterns in transported CPOC concentrations despite our predictions that maize detritus and filamentous algae would dominate the CPOC pool in winter (after crop harvest) and in late summer (onset of algal senescence), respectively. However, our field sampling was conducted during baseflow, and we may have missed the periodic sloughing events of filamentous algae and the inputs of maize detritus occurring during storm flows. For instance, we commonly observed large accumulations of maize detritus floating down streams during floods, primarily in the spring after snow melt (N. A. Griffiths, personal observation). While our sampling regime may not have captured the contribution of maize to transported CPOC in these hydrologically-variable streams, studies quantifying carbon stable isotope signatures in streams have been able to better characterize the contribution of maize. Specifically, the contribution of maize-derived C4 carbon to the transported particulate organic carbon pool of Midwestern streams increases after crop harvest (Munson and Carey 2004), as well as during floods (Dalzell et al. 2005). Thus, maize detritus and filamentous algae may make up significant portions of the transported particulate organic carbon pool at higher discharges, and this temporal variation deserves further study.

Components of benthic organic carbon

The benthic organic carbon pool (BOC) was fairly consistent across seasons and was relatively low (range: 41–241 g/m^2) in comparison to BOC standing stocks in less-modified, forested headwater streams in Quebec, Canada (150–399 g/m^2; Naiman et al. 1987), Oregon (117–710 g/m^2; Minshall et al. 1983), and Michigan (303–482 g/m^2; Minshall et al. 1983). Similar to transported organic carbon, we predicted that maize detritus and filamentous algae would comprise more of the BOC pool in winter and in summer, respectively. However, there were no seasonal patterns in CBOC or FBOC. While filamentous algae did not increase the overall CBOC pool, it still made up a considerable proportion of CBOC in early summer, comprising over 80% of the CBOC pool in half of the streams at a maximum standing stock of 19 g/m^2. Blooms of *Cladophora* quantified in these agricultural streams are typical of eutrophic waters (Dodds and Gudder 1992; Winter and Duthie 2000; Schaller et al. 2004). However, we are lacking basic information regarding the ecological role of *Cladophora* in agricultural streams, such as the controls (e.g., light, nutrients, flow) influencing summer algal growth and senescence, the decomposition dynamics of sloughed algal blooms, and the ability of algal mats to act as retention devices and retain organic matter during the low summer flows.

Maize detritus retained on the stream bottoms of the 6 agricultural streams was patchy, with samples collected in one stream in winter and two in late summer comprising 0.2–4.9% of the CBOC pool. As mentioned earlier, our field sampling was conducted during baseflow, and we likely missed the large, sporadic inputs and export of maize detritus that can occur during storms. Even during baseflow, the lack of retention features in agricultural stream channels may result in only short-term retention of maize detritus (Rosi-Marshall et al. 2007). We know little about the ecological roles of maize detritus in agricultural streams; however our previous research has shown that maize leaves decompose rapidly (breakdown rate = 0.015 day^{-1}; Griffiths et al. 2009) and are colonized within 3 days by macroinvertebrates (Chambers et al. 2010). Further research on the inputs, retention, and export of maize detritus during storm flows would be fruitful if we are to fully understand the fate of this material, especially when exported to downstream environments.

Across all seasons, grasses made up a considerable portion of the CBOC pool, with one stream (2B) having grasses comprising 81–100% of the CBOC pool. Grass buffer strips planted between the stream and crop fields are common in the agricultural Midwest, primarily due to incentives provided to farmers through the United States Department of Agriculture's Conservation Reserve Program. As the grasses senesce, they slump into the water column while remaining rooted to the banks, and thus grasses may not make up a large portion of the transported CPOC pool despite their prevalence in the CBOC pool. The ecological role of grasses in agricultural streams is understudied; however, Menninger and Palmer (2007) found that standing stocks of grasses in agricultural streams were similar to standing stocks of CBOC in forested streams, yet grasses tended to decompose faster than deciduous leaves. While our sampling regime did not focus on the growth and senescence of riparian grasses, these grasses may represent another important allochthonous resource to agricultural streams, and their importance in the organic carbon budget should be further investigated.

Organic carbon turnover

We found different seasonal patterns in heterotrophic respiration (R_{het}) depending on whether we used the whole-stream or substrate-specific method to measure R_{het}. Inputs of organic carbon can stimulate whole-stream respiration (Roberts et al. 2007), and if large inputs of organic carbon increased the CBOC pool (e.g., as senesced filamentous algae or maize detritus), we predicted R_{het} to increase in winter (after crop harvest) and in late summer (onset of algal senescence). However, there were no seasonal differences in whole-stream R_{het}, and R_{het} was not correlated with BOC standing stocks, but instead was positively related to stream water SRP concentrations. Multiple studies have found that whole-stream respiration is influenced by temperature (Bott et al. 1985; Sinsabaugh 1997; Uehlinger et al. 2000), nutrients (Mulholland et al. 2001), and organic carbon supply (Roberts et al. 2007); however, correlations between respiration rates and BOC standing stocks tend to be weak (e.g., Webster et al. 1995; Mulholland et al. 2001). This weak relationship may be due to the overriding influence of hyporheic respiration on whole-stream respiration and the inability of traditional sampling methods to quantify organic carbon in the hyporheic zone (Fellows et al. 2001). However, these channelized agricultural streams likely have small hyporheic zones (J. L. Tank, unpublished data). While R_{het} tended to be similar across seasons using the whole-stream method, there was a seasonal pattern in R_{het} using the substrate-specific method, with the lowest R_{het} rates occurring in winter and highest R_{het} rates found in late summer. The seasonal pattern with substrate-specific R_{het} was driven by differences in stream water temperature. The different factors influencing whole-stream vs. substrate-specific R_{het} (SRP vs. temperature, respectively) may reflect the different temporal and spatial scales that are integrated by these two methods.

Of the two different methods we used to quantify R_{het}, we opted to use the whole-stream approach to calculate carbon spiraling metrics as it integrated respiration of the entire stream reach, including decomposing maize detritus and filamentous algae, which would not be included in the substrate-specific method on fine organic particles. However, we did use R_{het} determined via both methods to examine how methodology influenced calculations of organic carbon spiraling. S_{OC} varied up to an order of magnitude depending on the R_{het} method used, yet seasonal patterns in S_{OC} were similar due to the overwhelming influence of discharge on spiraling metrics. Thus, organic carbon transport seems to override variability in organic carbon processing (as R_{het} and K_{OC}) in these channelized agricultural streams.

Organic carbon spiraling metrics

Organic carbon spiraling metrics incorporate both hydrologic transport and biological processing of organic carbon and thus represent an integrative metric describing the ecological fate of carbon in streams (Newbold et al. 1982; Minshall et al. 1992). The patterns of V_{OC} in these agricultural study streams changed seasonally, with faster transport rates occurring during autumn and winter and slower rates found in late summer. These patterns were driven by seasonal differences in discharge and were not influenced by changes in the benthic or transported organic carbon pools (see Eq. 1), suggesting that there is a strong hydrologic influence on the downstream transport of organic carbon. Larger streams and rivers tend to have higher V_{OC} rates compared to headwaters due to increased discharge and smaller BOC pools (Minshall et al. 1983; Naiman et al. 1987; Minshall et al. 1992). In our study, V_{OC} ranged from 1 to 483 m/d, and these values were similar to the range reported for the much larger Middle Snake River in Idaho (V_{OC} = 31–619 m/d; Q = 17,000–100,000 L/s), where flow regulation has caused organic rich sediments to accumulate on the benthos (Thomas et al. 2005). Thus, the similar V_{OC} values appear to reflect the larger BOC standing stocks in the Middle Snake River (435–1,672 g/m^2) compared to these agricultural streams (41–241 g/m^2). Similarly, V_{OC} in these agricultural streams (Q = 1–1,120 L/s) were faster than rates measured in Augusta Creek, Michigan (7.3–89.2 m/d), a similar-sized system (14–1,130 L/s) draining a relatively undisturbed forested watershed, as Augusta Creek had relatively larger BOC standing stocks (303–482 g/m^2; Minshall et al. 1983) than the 6 agricultural streams in this study. However, during low-flow periods (i.e., late summer), the 6 agricultural streams had V_{OC} values (1–12 m/d) that were similar to those measured in forested headwater streams. Thus, throughout most seasons, agricultural streams draining intensively-cultivated land in the Midwestern U.S. appear to transport organic carbon downstream more quickly compared to similar-sized forested systems. The combined influence of hydrology on downstream transport and smaller BOC standing stocks, reflecting decreased inputs and few retention devices, appear to influence V_{OC} in these agricultural streams. However, more research is needed to determine whether similar factors influence V_{OC} in streams draining other types of agriculture land (e.g., pastureland).

The index of retention (IR) is an alternate way to express the role of hydrology on organic carbon transport, and is defined as the ratio of the mean water velocity to the downstream velocity of organic carbon (see Eq. 4; Minshall et al. 1992). In these agricultural streams, IR varied seasonally with streams being the most retentive in late summer compared to all other seasons, and similar to V_{OC}, this variation was driven by seasonal differences in discharge. In placing IR values in the context of other studies, when the agricultural streams were most retentive of organic carbon in late summer (IR range = 1,008–2,912), IR values were comparable to the headwaters of the relatively undisturbed streams (Minshall et al. 1983, 1992). In comparison, the least retentive agricultural stream (2A) had an IR of 98 in winter (Q = 1,120 L/s) which was similar to IR in the Middle Snake River (IR = 96, Q = 89,208 L/s; Thomas et al. 2005) and the sixth- to eighth-order reaches of the Salmon River, Idaho (IR = 234, 23, respectively, Q = 30,000 L/s; Minshall et al. 1992), both much larger, western rivers. The variation in IR in agricultural streams demonstrates the overriding influence of hydrology on organic carbon transport. These streams can be as retentive as relatively undisturbed headwater streams during periods of low flow (i.e., late summer), but can also be as unretentive as large rivers that act more like conduits for organic carbon transport.

The fate of organic carbon in streams is determined by a combination of the transport dynamics discussed above and the rate of biological processing (K_{OC}). While these agricultural streams showed seasonal patterns in V_{OC}, K_{OC} did not differ seasonally. However, K_{OC} did vary almost two orders of magnitude among streams (0.0007–0.0193 day^{-1}), driven by variation primarily in R_{het} and secondarily in BOC. Further, the variation in R_{het} and thus K_{OC} was driven by differences in stream water SRP, suggesting that K_{OC} may be a sensitive metric to ambient water chemistry. Similarly, Naiman et al. (1987) found that K_{OC} was low (0.00002–0.0021 day^{-1}) in streams draining boreal forests in Quebec, Canada, reflecting a combination of low nutrient concentrations, cold water temperatures, and large amounts of refractory woody material that limited heterotrophic respiration. Further, K_{OC} tends to increase with stream size, due to an increase in R_{het} and a decrease in BOC standing stocks (Minshall et al. 1983; Naiman et al. 1987; Minshall et al. 1992). Interestingly, the range of K_{OC} values measured in low-order agricultural streams in the Midwestern U.S. (0.0007–0.0193 day^{-1}) was similar to the range measured along headwaters to mid-sized rivers in four biomes across the United States (0.0002–0.0143 day^{-1}; Minshall et al. 1983). Despite the lack of seasonality in K_{OC} and an apparent dominance of hydrology on the fate of organic carbon, the biological utilization of organic carbon is an important fate in agricultural streams, and the wide range in K_{OC} values suggests that the biological activity in these streams varies partially in response to differences in stream water SRP concentrations.

Organic carbon spiraling lengths (S_{OC}) displayed a seasonal pattern that mirrored the pattern seen in V_{OC}, namely the longest spiraling lengths occurred in winter and the shortest spiraling lengths occurred in late summer. Longer S_{OC} values in winter were a result of increases in discharge, as documented in previous studies (Minshall et al. 1983, 1992; Naiman et al. 1987; Meyer and Edwards 1990; Webster et al. 1995, 1999; Young and Huryn 1999). However, only discharge, and not any component of organic carbon pools (transported or benthic) or processing (heterotrophic metabolism) drove the seasonal patterns in S_{OC}, suggesting that hydrology tightly controls the fate of organic carbon in agricultural streams. Further, in comparing the efficiency of carbon utilization (S_{OC}) in these agricultural streams to primarily less-modified systems (Fig. 6), we show that at higher discharges, these channelized agricultural streams may be acting more like conduits for the downstream transport of organic carbon compared to more retentive reference systems.

Implications for coupled biogeochemical cycles

Headwater streams draining row-crop agriculture have been greatly modified through channelization and the addition of subsurface tile drainage in order to maximize drainage efficiency (Zucker and Brown 1998; Blann et al. 2009). The resulting effect on organic carbon dynamics appears to be a strong hydrologic control on the fate of organic carbon during baseflow, and stands in stark contrast to forested and more pristine headwaters that tend to be relatively retentive of organic carbon. Thus, throughout most of the year, these channelized agricultural streams with flashy hydrographs may act primarily as conduits for the downstream transport of organic carbon. In contrast, during low, stable-flow periods (i.e., late summer in this study), these streams can be as retentive of organic carbon as forested headwaters.

These periods of increased water residence time in late summer may be important for coupled carbon and nitrogen biogeochemical cycles. In agricultural streams, low-flow periods correspond to periods of high efficiency of stream water nitrate removal (up to $>100\%$ day^{-1}) via denitrification (Royer et al. 2004). Throughout the rest of the year, loss rates of nitrate via denitrification are much lower (generally $<5\%$ day^{-1}) (Royer et al. 2004), and the resultant large nitrate loads that leave agricultural headwaters can have damaging downstream effects (Goolsby et al. 2001; Rabalais et al. 2002). Organic carbon is required for microbially-mediated denitrification to reduce nitrate to dinitrogen gas, and thus, during low-flow periods, the combined influence of nitrate-rich stream water and increased organic carbon retention may fuel denitrification. Further, previous studies have demonstrated that streams with longer water residence times have elevated denitrification rates (Opdyke et al. 2006; Kaushal et al. 2008). In Midwestern agricultural streams, a restoration strategy is being implemented, where small floodplains are being created and connected to the incised, trapezoidal main channel to dissipate water velocities during high flows. The floodplains promote bank stability and provide erosion control (Landwehr and Rhoads 2003; Evans et al. 2007; Powell et al. 2007), and may also result in a longer residence time for excess nitrate to be denitrified (S. S. Roley, unpublished data). We show here that organic carbon would be available during low-flow periods to fuel denitrification. If denitrification rates increase in these restored agricultural streams, more carbon will be respired to CO_2, and agricultural streams may become a larger source of CO_2 to the atmosphere. Further evaluating the role of agricultural streams as processors and/or conduits of organic carbon, as well as examining the interactions of coupled biogeochemical cycles that influence organic carbon processing (i.e., denitrification), will be necessary in order to understand how small streams influence estimates of carbon cycling in inland waters at both regional and global scales (Cole et al. 2007; Battin et al. 2009).

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