Decomposition of maize leaves and grasses in restored agricultural streams

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Abstract. Headwater streams draining row-crop agriculture receive allochthonous inputs of maize detritus and grasses, but organic matter (OM) processing is not well studied in agricultural streams. Agricultural streams in the midwestern USA have incised, trapezoidal channels that retain less particulate OM than forested streams. The 2-stage ditch is a restoration strategy in which small floodplains are constructed and connected to stream channels to increase channel stability and decrease erosion. Microbial decomposition may be higher on restored floodplains because water residence times are longer than on the steep banks of trapezoidal streams. We examined decomposition of maize leaves (*Zea mays*), native rice cutgrass (*Leersia oryzoides*), and invasive reed canary grass (*Phalaris arundinacea*) in 4 restored streams. We measured breakdown rates in the main channel of upstream control reaches (incised, trapezoidal channel), the main channel of downstream treatment reaches (restored with constructed floodplains), steep control banks, and treatment floodplains. OM decomposed faster in channels than on banks and floodplains, and maize decomposed faster (stream $k = 0.0160/d$, riparian $k = 0.0040/d$) than rice cutgrass (stream $k = 0.0065/d$, riparian $k = 0.0018/d$) and reed canary grass (stream $k = 0.0036/d$, riparian $k = 0.0014/d$) probably because lignin and N content differed. Breakdown rates varied among streams because of differences in shredder density (primarily Isopoda: *Lirceus* and *Caecidotea*) and water temperature. Floodplain restoration did not affect breakdown rates. Floodplains of 3 streams were inundated longer than steep banks in upstream control reaches, but breakdown rate and inundation duration were not related. However, OM must be retained within the stream to be available for decomposition. Thus, the floodplains may promote the retention of OM, and ultimately, incorporation of maize and grasses into headwater-stream food webs.

Key words: allochthonous inputs, organic matter, detritus, litter, corn, breakdown, decomposition, agriculture, restoration, floodplain, isopods.

Organic matter (OM) decomposition is a fundamental ecosystem process that fuels stream food webs by making energy and nutrients in detritus available to consumers. Most stream decomposition studies were done in temperate forested headwaters (Kaushik and Hynes 1971, Petersen and Cummins 1974, Webster et al. 1999, Tank et al. 2010a) that receive allochthonous inputs from the riparian zone (Fisher and Likens 1973, Benfield 1997, Wallace et al. 1997, 1999). However, many landscapes are used for agriculture (i.e., planting crops and raising livestock) (Tilman et al. 2001, Lubowski et al. 2006), and detrital decomposition in streams draining these agricultural catchments is not well understood.

Agricultural streams are affected by multiple stressors, including riparian clearing, channelization, increased bank erosion and sedimentation, nutrient enrichment, and pesticide and herbicide contamination (Cooper 1993, Allan 2004), and these extrinsic factors can alter the processing of organic detritus. For example, OM may decompose more quickly in agricultural streams than in less-affected systems if nutrient-rich stream water fuels microbial processing of leaf litter (Hagen et al. 2006, Paul et al. 2006, Griffiths et al. 2009) or if flashy discharge promotes physical abrasion of detritus (Tuchman and King 1993). However, OM may decompose more slowly in agricultural streams with low shredder densities

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848

(Benfield et al. 1977, Stone et al. 2005, Hagen et al. 2006, Chambers et al. 2010) or high rates of sedimentation that bury benthic detritus (Sponseller and Benfield 2001, McTammany et al. 2008). Thus, the effects of agriculture on detrital decomposition are not generalizable (Huryn et al. 2002, Hagen et al. 2006), but depend on stream-specific physical, chemical, and biological characteristics.

OM decomposition rates also are affected by the intrinsic characteristics (e.g., lignin, tannin, N content) of riparian plant species that enter streams (Webster and Benfield 1986, Ostrofsky 1997, Webster et al. 1999, LeRoy and Marks 2006, Ardón et al. 2009). However, most studies of agricultural streams have addressed decomposition of leaves from trees found in temperate forests rather than detritus common in riparian zones of open-canopied agricultural streams (e.g., crop detritus, grasses). Maize (*Zea mays* L.) is the dominant crop cultivated in the USA (NASS 2009), and planting occurs primarily in the midwestern Corn Belt states (e.g., Indiana, Illinois, Iowa, Nebraska). In areas where conservation tillage is practiced, most of the maize plant (leaves, husks, stalks, cobs) is left on the soil surface after crop harvest and can blow or wash into adjacent streams (Stone et al. 2005, Rosi-Marshall et al. 2007, Jensen et al. 2010, Tank et al. 2010b). Inputs and standing stocks of maize detritus in agricultural streams are typically 1 to 2 orders of magnitude lower than those in temperate forested headwaters (Benfield 1997, Webster and Meyer 1997). Few investigators have measured maize breakdown in streams, and they focused primarily on the influence of genetic modification on breakdown rates (Rosi-Marshall et al. 2007, Griffiths et al. 2009, Swan et al. 2009, Chambers et al. 2010) rather than on broader factors (intrinsic and extrinsic) controlling maize decomposition.

Riparian grasses are another important allochthonous input to midwestern agricultural streams (Niyogi et al. 2003, Stone et al. 2005, Menninger and Palmer 2007, Griffiths et al. 2012). Grasses grow between the active stream channel and the crop field and enter streams by slumping into the channel while still rooted in the banks. Standing crops of grass in agricultural streams are comparable to detrital standing stocks in temperate forested streams (Stone et al. 2005, Menninger and Palmer 2007). Breakdown rates of grasses have been measured in agricultural streams in New Zealand (Niyogi et al. 2003) and in the eastern USA (Menninger and Palmer 2007), but the intrinsic and extrinsic factors regulating the decomposition of grasses in streams draining intensive agriculture in the midwestern USA have not been reported.

Whether allochthonous detritus is decomposed near its point of entry or further downstream depends on the ability of stream reaches to retain OM inputs (Webster et al. 1994, 1999, Tank et al. 2010a). Streams draining row-crop agriculture in the midwestern USA have little riparian woody vegetation. Thus, in-stream structures that retain OM (e.g., large wood, tree roots, debris dams) (Bilby and Likens 1980, Ehrman and Lamberti 1992, Cordova et al. 2008) are absent. Moreover, these channelized, incised agricultural streams (Fig. 1A) are susceptible to erosion and bank slumping and must be dredged to maintain efficient drainage. As a result of frequent dredging, agricultural headwaters tend to be less retentive of organic C than forested streams (Griffiths et al. 2012). An alternative configuration to the managed trapezoidal channel is the 2-stage ditch (Powell et al. 2007b). This practice involves constructing small floodplains adjacent to the incised main channel (Fig. 1B) to decrease water velocity and promote deposition of fine sediments during high flows. The primary goal of this 2-stage restoration is to stabilize the channel and provide erosion control (Landwehr and Rhoads 2003, Evans et al. 2007, Powell et al. 2007a, b). In addition, OM may decompose faster on inundated restored floodplains than on the banks of unretentive, channelized streams that currently drain most of the agricultural Midwest.

We quantified breakdown rates of the dominant forms of allochthonous OM in streams draining intensive row-crop agriculture and examined whether floodplain restoration altered breakdown rates. We measured breakdown rates of 3 types of litter common in midwestern agricultural streams: maize leaves (*Zea mays* L.), native rice cutgrass (*Leersia oryzoides* (L.) Swartz), and reed canary grass (*Phalaris arundinacea* L.), which has become an aggressive invader in the region (Lavergne and Molofsky 2004). We also measured microbial activity, macroinvertebrate density, and OM chemistry (lignin, C, and N content) of decomposing litter to examine the extrinsic and intrinsic factors potentially controlling breakdown rates.

We assessed the effect of the 2-stage restoration on decomposition by measuring breakdown rates of all 3 OM types in the main channel and floodplains of 4 restored streams. Specifically, we measured breakdown rates in the main channel of the upstream control reaches (conventionally maintained, trapezoidal channel), the main channel of the downstream treatment reaches (2-stage restoration with adjacent constructed floodplains), steep control banks, and restored floodplains. We refer to the bank and floodplain habitats together as riparian habitat. We predicted that breakdown rates would be faster in the stream channel than in the riparian habitats. We also predicted that breakdown rates would be faster on the restored floodplains than the steep upstream banks
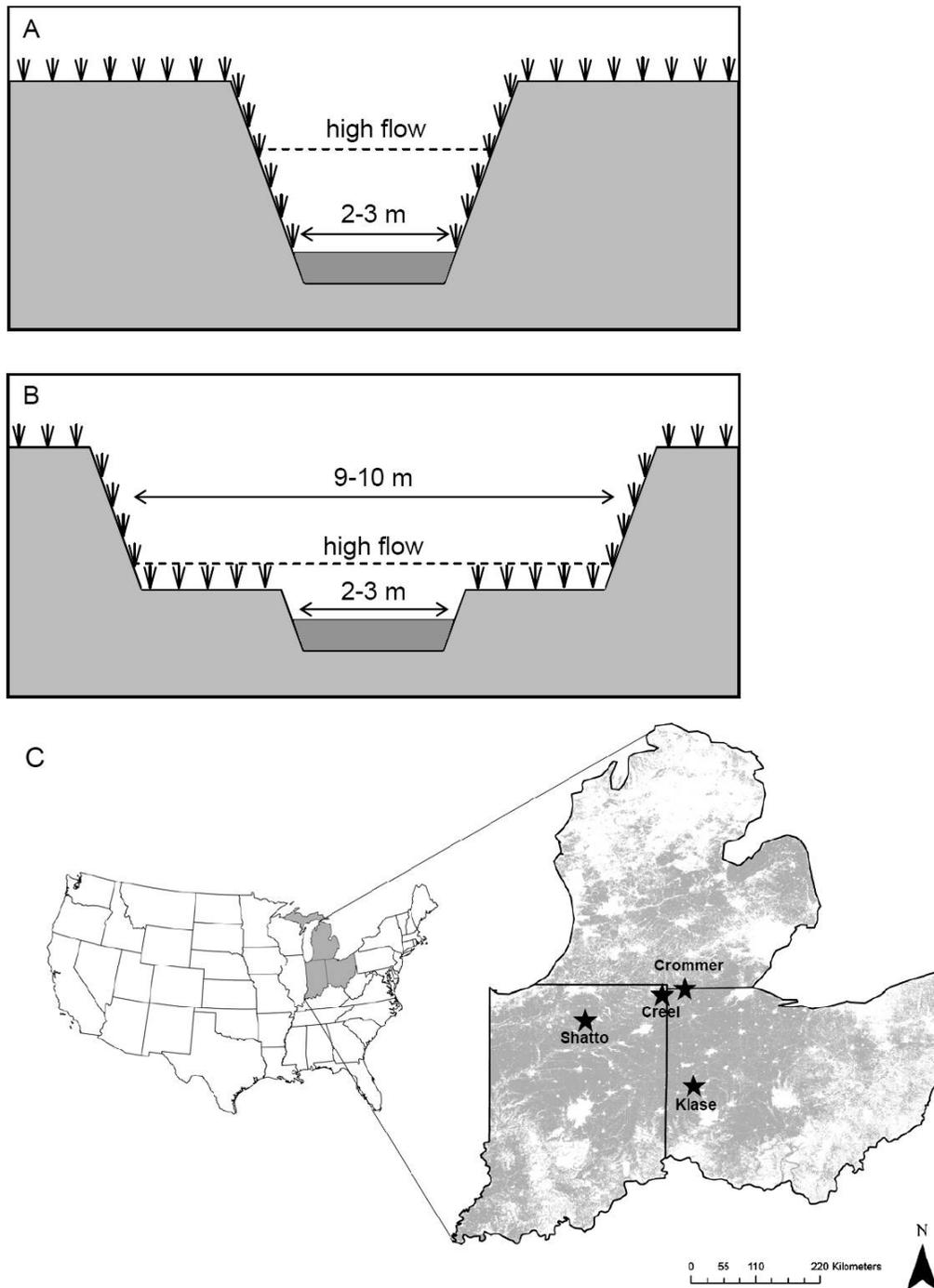
FIG. 1.   Diagram of an agricultural stream with a trapezoidal stream channel and steep banks (control reach in this experiment) (A), a restored agricultural stream with constructed floodplains that are connected to the main channel (treatment reach in this experiment) (B), and a map of the 4 study sites (Creel Creek, Crommer Creek, Klase Creek, and Shatto Creek) in the Corn Belt states of Indiana, Ohio, and Michigan, USA (C). Grey shading represents agricultural land use (cultivated crops and pasture).

because longer water residence times on restored floodplains would promote microbial processing of OM.

Methods

Study sites

We studied four 1st-order streams (Creel Creek, Crommer Creek, Klase Creek, and Shatto Creek) in the Corn Belt states of Indiana, Michigan, and Ohio, USA (Fig. 1C). Creel Creek and Crommer Creek are in the St. Joseph/Upper Maumee watersheds that drain into Lake Erie, and Klase Creek and Shatto Creek are in the Upper Miami and Tippecanoe watersheds, respectively, that drain into the Ohio River (Mississippi River Basin). The primary land use in the region is row-crop agriculture (Fig. 1C) in a maize–soybean rotation. The study sites are typical of low-gradient, midwestern agricultural streams in that they have sand/silt-dominated beds consisting of mainly run/pool sequences, grasses growing on the stream banks, and high NO_3^- concentrations as a result of fertilizer runoff from fields (Table 1). Historically, the trapezoidal shape of these streams (Fig. 1A) was maintained through regular dredging, resulting in erosion-prone, steep banks, and incised channels. However, a reach on each stream was restored with the 2-stage approach 1 to 4 y (Table 1) before our study. The 4 restored reaches are similar in length (600–1400 m), and the constructed floodplains are ~3.5 m wide on each side of the stream channel (Fig. 1B, Table 1). Vegetation was present on the banks and floodplains during our study, and rice cutgrass (*Leersia oryzoides*) and reed canary grass (*Phalaris arundinacea*) were 2 of the dominant grass species in these riparian habitats. Water residence time and water depth tend to differ between the restored floodplains and the steep banks. During high-flows (e.g., storms), the restored floodplains tended to be inundated for longer but water depth was shallower than on the steep banks (Fig. 2).

Breakdown of maize leaves and grasses

We used standard litterbag techniques (Benfield 2006) to quantify the breakdown rates of maize (*Zea mays*) leaves and grasses. Prior to crop harvest in mid-October 2009, we collected senescent maize leaves from a maize field beside Shatto Creek and senescent rice cutgrass and reed canary grass from the floodplains and banks of Shatto Creek. In the laboratory, we air-dried OM for 1 wk before constructing litterbags. We placed 13.0 ± 0.1 g of maize leaves or grasses (stems and blades in the proportion found in

TABLE 1. Physical and chemical characteristics of 4 restored agricultural streams in Indiana, Michigan, and Ohio, USA. Discharge, water velocity, and dissolved nutrients (NO_3-N, NH_4-N, and soluble reactive P [SRP]) were measured on each sampling date. Mean baseflow discharge and mean baseflow velocity were calculated on the days when the riparian habitats were not inundated.

| Stream name	Year of restoration	Length of restored reach (m)	Mean constructed floodplain width (m)	Stream slope (%)	Mean baseflow discharge (L/s)	Mean baseflow velocity (m/s)	NO_3-N range (mg N/L)	NH_4-N range (µg N/L)	SRP range (µg P/L)
Creel	2008	1400	3.6	0.32	31	0.04	0.2–1.5	6.4–62.4	6.3–35.1
Crommer	2003	640	3.6	0.04	62	0.07	0.8–4.6	43.6–1826.0	8.7–129.3
Klase	2005	600	3.5	0.20	15	0.03	3.2–13.9	38.4–321.1	6.4–325.4
Shatto	2007	600	3.2	0.16	92	0.10	4.6–7.5	27.2–92.1	8.1–46.5
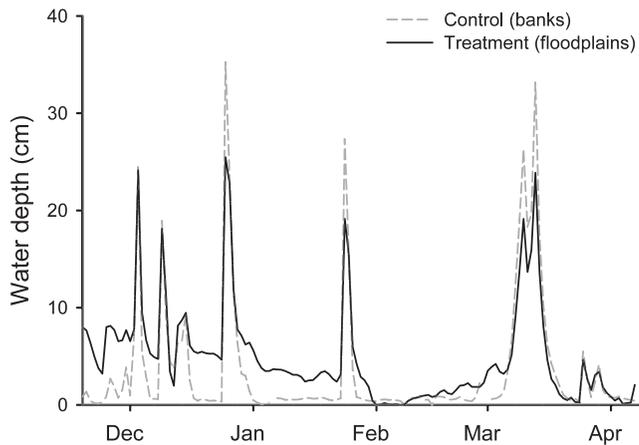
Fig. 2. Water depth (cm) on the control banks and treatment floodplains of Creel Creek over the study period.

the field) in nylon mesh bags (30 × 20 cm) that had a 1 × 0.25-cm mesh size (Volm Companies Inc., Antigo, Wisconsin) to allow invertebrates access to OM. We used the stems and blades of grasses because the entire plant decomposes in riparian and stream habitats. Thus, this approach provided a more realistic estimate of grass breakdown rates than using only blades. In each stream, we anchored 18 litterbags of each OM type in each of 4 habitat types: the main channels of the upstream control and downstream treatment reaches, and the steep control banks and restored treatment floodplains. We placed the stream-channel litterbags in areas of similar water velocity and placed the riparian litterbags on the banks and floodplains at equivalent heights (10–20 cm) above the baseflow waterline. We deployed the litterbags on 18–19 November 2009 and retrieved 3 replicate litterbags of each OM type from each habitat on days 5, 15, 30, 49, 70, 103, and 140 (n = 864 bags). To account for handling loss, we deployed and retrieved 5 replicates of each OM type from each stream on day 0 (n = 60). We conducted this experiment in late autumn through early spring because this period coincided with crop harvest and inputs of maize detritus (Rosi-Marshall et al. 2007, Jensen et al. 2010) and grass senescence and slumping into agricultural stream channels (NAG, personal observation). On day 49, we collected only in-stream samples, and on day 140, we collected only riparian (i.e., bank and floodplain) samples to characterize more accurately the decomposition dynamics of OM in these 2 habitat types. On each collection date, we transferred litterbags into prelabeled plastic bags, transported samples to the laboratory on ice, and either processed the samples immediately or froze them. We removed a subsample of OM from each litterbag collected from Shatto Creek

for use in a microbial respiration assay (described below) before freezing the samples.

We rinsed litterbags over a 1-mm-mesh sieve to remove sediments and invertebrates. On days 15 and 49, we collected all macroinvertebrates captured on the 1-mm-mesh sieve and stored samples in 80% ethanol for enumeration and identification. We counted invertebrates on days 15 and 49 to assess invertebrate colonization dynamics. We identified all aquatic shredding macroinvertebrates to the lowest level necessary to classify as a shredder-detritivore (usually family or genus) with keys published by Merritt et al. (2008) and Pennak (1989).

We put the rinsed OM into prelabeled paper bags, dried it at 60°C for 48 h, recorded total mass, and subsampled for measurement of ash-free dry mass (AFDM). We removed ~0.5 to 1.0 g of each sample, dried it at 60°C for 48 h, and combusted it in a muffle furnace at 550°C for 2 h. We calculated AFDM as the difference between the ash mass and the dry mass, and calculated the breakdown coefficient (k; /d) as ln(% AFDM remaining) vs time (Benfield 2006) for each OM type in each stream, reach (control, treatment), and habitat type (stream, riparian).

Microbial respiration on maize leaves and grasses

We assayed microbial respiration on maize, rice cutgrass, and reed canary grass collected from litterbags at Shatto Creek to compare microbial activity among OM types and between stream and riparian habitats. We measured microbial respiration on OM at only one stream, so these results do not represent a broad examination of the effects of restoration on this process.

After field collection, we removed ~4 cm² of maize leaves or grasses from each bag and lightly washed the OM samples with stream water to remove adhering sediments and invertebrates. We placed OM into 60-mL Falcon tubes filled (no air bubbles) with filtered stream water (GF/F, 0.7-µm pore size; Whatman, Florham Park, New Jersey). We incubated all samples collected from the riparian litterbags in filtered stream water to simulate flooded conditions. We measured microbial respiration at 2 temperatures: room temperature (20°C) to compare rates directly among sampling dates, and at ambient stream water temperature (1–8°C) in a low-temperature incubator (Fisher Scientific, Pittsburgh, Pennsylvania) to compare in situ rates. On the 1st retrieval date (day 5), we measured microbial respiration only at room temperature. To quantify microbial respiration on OM (expressed as mg O_2 g^{-1} AFDM h^{-1}), we measured the change in dissolved O_2 (DO) concentration over a

2-h incubation period in the dark using a hand-held DO sensor (DO200; Yellow Springs Instruments, Yellow Springs, Ohio). We included tubes containing only filtered stream water as controls ($n = 3$/sampling date) to account for background changes in DO, which were minimal.

Tissue chemistry of maize leaves and grasses

We determined the nutritional quality of each OM type from litterbags on days 0, 30, and 103 by measuring the lignin content (expressed as % dry mass) with near-infrared reflectance spectroscopy analyzed at the Dairy One Forage Testing Laboratory (Ithaca, New York), and the C and N content (expressed as % dry mass) with a Costech Elemental Analyzer (Costech Analytical Technologies, Valencia, California). Lignin analysis required ~5 g of OM, so we pooled all 3 replicates of each OM type from each reach, habitat, and stream for the analysis. For C and N analysis, we used ~0.5 g of dry mass from pooled samples. We ground samples to a fine powder with an electric grinder followed by a mortar and pestle and placed ~3 mg of each sample into a 5 × 7-mm Sn capsule for elemental analysis. We determined concentrations of C and N in OM using a 5-point calibration curve of acetanilide.

Water chemistry, air and water temperature, water depth, and discharge

To compare nutrient concentrations among study streams, we collected water samples on each sampling date from the control and treatment reaches in each stream. We filtered water samples (GF/F) into acid-washed, polypropylene bottles, and froze the samples at $-30°C$ until analysis. We measured NO_3-N concentrations using the Cd-reduction method (APHA 1995), NH_4-N concentrations using the phenol-hypochlorite method (Solorzano 1969), and soluble reactive P (SRP) concentrations using the molybdate-antimony method (Murphy and Riley 1962) on a Lachat QC8500 Flow Injection Autoanalyzer (Lachat Instruments, Loveland, Colorado).

We measured air temperature every hour with a HOBO temperature logger (Onset, Bourne, Massachusetts) that we placed in the grass buffer strip between the control and treatment reaches of each stream. We measured water temperature hourly in each stream using Hydrolab MS5 data-logging sondes (Hach Hydromet, Loveland, Colorado) that we placed at the bottom of both the control and treatment reaches. Water temperature loggers failed during some months of the study, thereby restricting our comparisons of water temperature among streams

and precluding calculation of breakdown rates per degree day.

We monitored inundation of control banks and treatment floodplains with capacitance water-level probes (Odyssey, Christchurch, New Zealand) that logged water depth every 10 min throughout the study period. From these data, we calculated the duration (in d) of inundation of banks and floodplains. Specifically, we considered the riparian habitats to be inundated when the water depth was >5 cm because litterbags would be submerged at this water level. On each collection date, we measured water velocity at the bottom of each study reach with a velocity meter (Marsh–McBirney Flow-Mate, Frederick, Maryland) and calculated discharge based on the velocity–area protocol (Gore 2006).

Statistical analyses

We used a 3-way analysis of covariance (ANCOVA) blocked by stream, with time as the covariate, and with ln(% AFDM remaining) as the dependent variable to compare breakdown rates among OM types, habitats, and reaches. We used a 4-way repeated measures (rm) analysis of variance (ANOVA) to test for changes in microbial respiration rates over time and among OM types, habitats, reaches, and incubation temperatures. We ran microbial respiration assays on all OM collected throughout the experiment at Shatto Creek, but respiration data from only 4 days (15, 30, 70, and 103) were used in the rm ANOVA because these were the 4 dates on which microbial respiration was measured in both habitats and at both incubation temperatures.

We compared shredder density on the 3 OM types and between control and treatment reaches with a 2-way ANOVA blocked by stream on each collection date/habitat combination (day 15 stream, day 15 riparian, day 49 stream). We used a 3-way rmANOVA blocked by stream to test for changes in OM tissue chemistry over time (days 0, 30, 103) and among OM matter types, habitats, and reaches. When main effects were significant, we used Tukey's Honestly Significant Difference (HSD) post hoc tests to identify factors that differed.

We used ANCOVA and linear regression to identify the intrinsic and extrinsic factors controlling breakdown rates among streams, habitats, and OM types. To examine the extrinsic factors affecting breakdown rates among streams, we used ANCOVA on breakdown rates with OM type as a factor, the extrinsic variable as the covariate, and breakdown rate as the dependent variable. If necessary, we normalized data to meet parametric assumptions
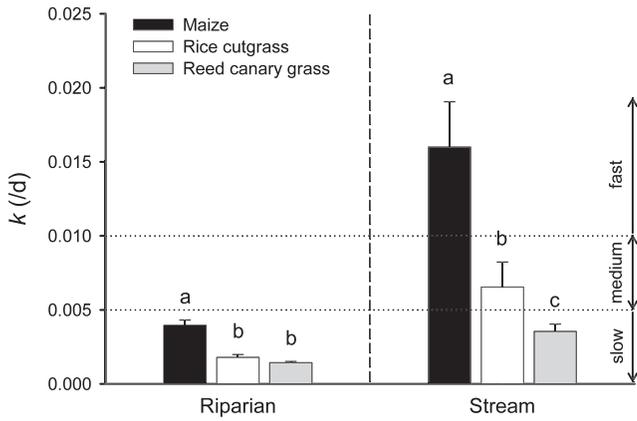
FIG. 3. Mean breakdown rates (k; /d) (+1 SE; $n = 4$) of maize leaves, rice cutgrass, and reed canary grass in the stream channel and riparian habitats in 4 agricultural streams. Bars with the same letters are not significantly different within habitat types (Tukey's Honestly Significant Difference, $p > 0.05$). The dotted horizontal lines represent Petersen and Cummins' (1974) litter processing classification scheme of fast ($k > 0.01$/d), medium ($0.005 < k < 0.01$/d), and slow ($k < 0.005$/d) decomposing leaf species in aquatic ecosystems.

using $\ln(x)$ or $\sqrt{(x)}$ transformations. We used SYSTAT (version 12.0; Systat Software, San Jose, California) for all data analyses.

Results

Breakdown rates of maize leaves and grasses

OM decomposed faster in the stream channel than in the riparian (bank and floodplain) habitats (ANCOVA, $F_{1,309} = 135.4$, $p < 0.0001$; Fig. 3), and differences in breakdown rates among the 3 OM types depended on whether litterbags were in the stream channel or in the riparian habitats (OM type $\times$ habitat interaction, $F_{2,309} = 27.9$, $p < 0.0001$). In the stream channels, maize leaves decomposed fastest, rice cutgrass decomposed at an intermediate rate, and reed canary grass decomposed slowest (Tukey's HSD, all $p < 0.05$; Fig. 3, Table 2). In the riparian habitats, maize decomposed faster than both grasses (Tukey's HSD, all $p < 0.05$), and rice cutgrass and reed canary grass decomposed at similar rates (Tukey's HSD, $p = 0.99$; Fig. 3, Table 2). Breakdown rates were more variable in stream channels (coefficient of variation [CV] = 75%) than in the riparian habitats (CV = 54%), and relationships between mass loss and incubation time were stronger for OM decomposing in stream channels (median $r^2 = 0.84$, all $p < 0.05$) than in riparian habitats (median $r^2 = 0.73$, all $p < 0.05$).

Breakdown rates differed between the stream and riparian habitats, but not between treatment and

TABLE 2. Breakdown rates (k; /d) of maize leaves, rice cutgrass, and reed canary grass in the stream channel and riparian habitats in upstream control (steep banks) and downstream treatment (restored floodplains) reaches and mean ±1 SE breakdown rate of each organic matter type in 4 restored agricultural streams.

| Stream name	Treatment	Breakdown rate in the stream channel (/d)			Breakdown rate in the riparian habitat (/d)		
		Maize	Rice cutgrass	Reed canary grass	Maize	Rice cutgrass	Reed canary grass
Creel	Control	0.0126	0.0052	0.0037	0.0033	0.0019	0.0013
	Treatment	0.0130	0.0047	0.0026	0.0031	0.0026	0.0011
Crommer	Control	0.0093	0.0042	0.0024	0.0035	0.0015	0.0013
	Treatment	0.0110	0.0041	0.0028	0.0042	0.0014	0.0016
Klase	Control	0.0192	0.0057	0.0032	0.0061	0.0025	0.0017
	Treatment	0.0146	0.0053	0.0039	0.0037	0.0014	0.0014
Shatto	Control	0.0280	0.0111	0.0053	0.0036	0.0013	0.0015
	Treatment	0.0203	0.0120	0.0045	0.0042	0.0018	0.0016
Mean		0.0160 ± 0.0031	0.0065 ± 0.0017	0.0036 ± 0.0005	0.0040 ± 0.0004	0.0018 ± 0.0002	0.0014 ± 0.0001
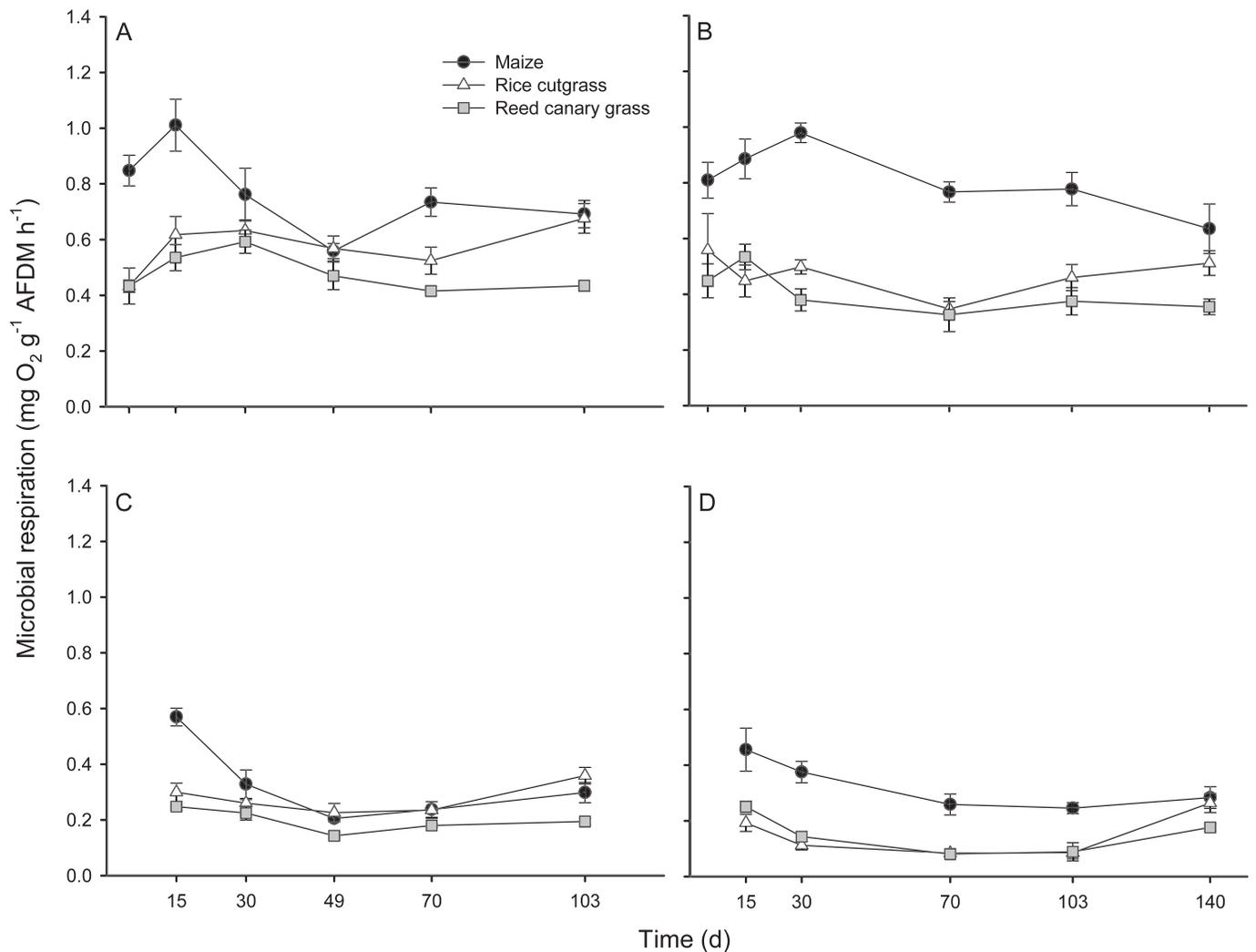
FIG. 4. Mean ($\pm$1 SE) microbial respiration rates (mg O_2 g^{-1} ash-free dry mass [AFDM] h^{-1}) on maize leaves, rice cutgrass, and reed canary grass in the stream channel (A, C) and in the riparian habitats (B, D) of Shatto Creek. Organic matter was incubated at room temperature (20°C) (A, B) and at ambient stream water temperature (1–8°C) (C, D).

control stream reaches (reach, $F_{1,309} = 1.8$, $p = 0.17$; reach $\times$ habitat, $F_{1,309} = 0.4$, $p = 0.52$). Breakdown rates varied significantly among streams ($F_{3,309} = 18.6$, $p < 0.0001$). The fastest stream-channel breakdown rates were in Shatto Creek and the slowest in Crommer Creek (Table 2).

Microbial respiration on maize leaves and grasses

Microbial respiration rates differed among the 3 OM types through time, depending on whether litterbags were incubated in the stream channel or in the riparian habitat of Shatto Creek (rmANOVA, OM type $\times$ habitat interaction, $F_{6,126} = 3.5$, $p = 0.003$; Fig. 4A–D). In the riparian habitat, microbial respiration rates were higher on maize than on rice cutgrass and reed canary grass throughout the litterbag

incubation period (Fig. 4B, D), but in the stream channel, rates were not consistently different among species (Fig. 4A, C). In the stream channel, rates on maize were initially 2$\times$ as high as rates on the 2 grasses. However, because maize decomposed rapidly in Shatto Creek (Table 2), by day 30, most of the OM that remained in the litterbags was recalcitrant material (i.e., leaf veins) that supported low rates of microbial activity.

Respiration rates were higher at room temperature (20°C, Fig. 4A, B) than at ambient stream temperature (1–8°C) ($F_{1,42} = 549.1$, $p < 0.0001$; Fig. 4C, D). Nevertheless, the temporal patterns of respiration rates were similar at both temperatures ($F_{3,126} = 1.5$, $p = 0.21$; Fig. 4A–D). Microbial respiration rates differed significantly between the treatment and control reaches over

time (time $\times$ reach $\times$ habitat interaction, $F_{3,126} = 2.9$, $p = 0.04$). However, this pattern was caused by differences in respiration rates in the control and treatment stream channels rather than differences in respiration rates on the banks and floodplains. Respiration rates were initially higher in the treatment stream channel than the control stream channel, and this pattern switched by the end of the incubation period.

Shredders on maize leaves and grasses

Shredder density on stream-channel litterbags differed among OM types (ANOVA, day 15: $F_{2,15} = 6.8$, $p = 0.008$, day 49: $F_{2,15} = 5.0$, $p = 0.02$; Fig. 5A, B), with higher shredder density on maize leaves than on rice cutgrass and reed canary grass (Tukey's HSD, all $p < 0.05$). Shredder density was similar on rice cutgrass and reed canary grass on both dates (Tukey's HSD, day 15: $p = 0.58$, day 49: $p = 0.98$). In contrast, in the riparian habitats, shredder density did not differ among OM types on day 15 ($F_{2,15} = 0.7$, $p = 0.49$; Fig. 5C). Shredder density did not differ between the treatment and control stream reaches (day 15: $F_{1,15} = 0.4$, $p = 0.53$, day 49: $F_{1,15} = 0.7$, $p = 0.41$) or between the bank and floodplain habitats ($F_{1,15} = 2.1$, $p = 0.17$).

Shredder density on litterbags varied among streams (ANOVA, day 15: stream $F_{3,15} = 67.9$, $p < 0.0001$, day 49: stream $F_{3,15} = 20.0$, $p < 0.0001$, day 15: riparian $F_{3,15} = 14.0$, $p = 0.0001$; Fig. 5A–C). The highest density was on stream-channel litterbags in Shatto Creek and the lowest was on stream-channel litterbags in Creel and Crommer Creeks on day 15 (Fig. 5A). Similar patterns among streams occurred on day 49. However, shredder density was highest on maize detritus in Klase Creek (Fig. 5B). The riparian habitats of the 4 study streams were inundated on day 15, and aquatic shredders were present in these litterbags (Fig. 5C), albeit at a much lower density than in the stream-channel litterbags on the same date (Fig. 5A).

The higher shredder densities in Klase and Shatto Creeks were largely the result of high densities of the shredding isopods *Lirceus* and *Caecidotea* (Isopoda: Asellidae), respectively. *Lirceus* and *Caecidotea* accounted for 96% of all shredders associated with litterbags in these 2 streams. Other shredders were present in litterbags at a much lower density and included stoneflies (Capniidae), case-building caddisflies (Lepidostomatidae, Limnephilidae, and Phryganeidae [*Ptilostomis*]), and cranefly larvae (Tipulidae).

Tissue chemistry of maize leaves and grasses

Initial lignin content (day 0) differed among OM types. Maize leaves and rice cutgrass had lower lignin content than reed canary grass (Fig. 6A, B). OM lignin

content increased over time (rmANOVA, $F_{2,66} = 65.3$, $p < 0.0001$), and this increase was less pronounced for OM decomposing in the riparian habitats (Fig. 6B) than OM decomposing in the stream channel ($F_{2,66} = 19.8$, $p < 0.0001$; Fig. 6A).

Initial C:N ratios (day 0) also differed among OM types. Maize leaves had lower C:N than reed canary grass and rice cutgrass (Fig. 6C, D). The differences in initial C:N were caused by differences in initial % N content. Maize leaves had higher % N content than reed canary grass and rice cutgrass (Fig. 6E, F). C:N changed over time, and different temporal patterns emerged among OM types and habitats (rmANOVA, $F_{4,66} = 3.4$, $p = 0.01$). C:N of maize leaves initially increased then leveled off, whereas C:N of the 2 grasses decreased over the litterbag incubation period (Fig. 6C, D), with a greater decrease in C:N of rice cutgrass in stream habitats over time (Fig. 6C). The temporal changes in C:N were mainly caused by changes in % N rather than % C because % N mirrored the temporal pattern of C:N. Percent N in maize leaves decreased then leveled off, whereas % N in the 2 grasses increased over the deployment period (Fig. 6E, F).

Factors influencing breakdown rates among streams and OM types

Extrinsic drivers of breakdown rates in stream channels.—Variation in breakdown rates among streams was driven by differences in shredder density (ANCOVA, $F_{1,6} = 22.9$, $p = 0.003$) and stream water temperature (ANCOVA, $F_{1,6} = 37.9$, $p = 0.0008$). When OM types were considered individually, strong relationships between breakdown rate and shredder density were found in each stream (simple linear regressions, day 15 maize: $r^2 = 0.92$, $p = 0.04$, day 15 rice cutgrass: $r^2 = 0.66$, $p = 0.19$, day 15 reed canary grass: $r^2 = 0.91$, $p = 0.04$; Fig. 7). Positive relationships also were found between breakdown rate and water temperature (maize: $r^2 = 0.86$, $p = 0.07$, rice cutgrass: $r^2 = 0.99$, $p = 0.003$, reed canary grass: $r^2 = 0.88$, $p = 0.06$). However, shredder density and water temperature were strongly correlated (maize: $r = 0.99$, $p = 0.002$, rice cutgrass: $r = 0.99$, $p = 0.009$, reed canary grass: $r = 0.99$, $p = 0.004$), so assessing the extent to which water temperature and shredder density interacted to influence OM decomposition was difficult. Breakdown rates were not related to any measure of water chemistry (all $p > 0.05$).

Extrinsic drivers of breakdown rates in riparian habitats.—Inundation duration of riparian habitats varied from 1 to 48 d among streams. In Klase, Shatto, and Creel Creeks (Fig. 2), floodplains were
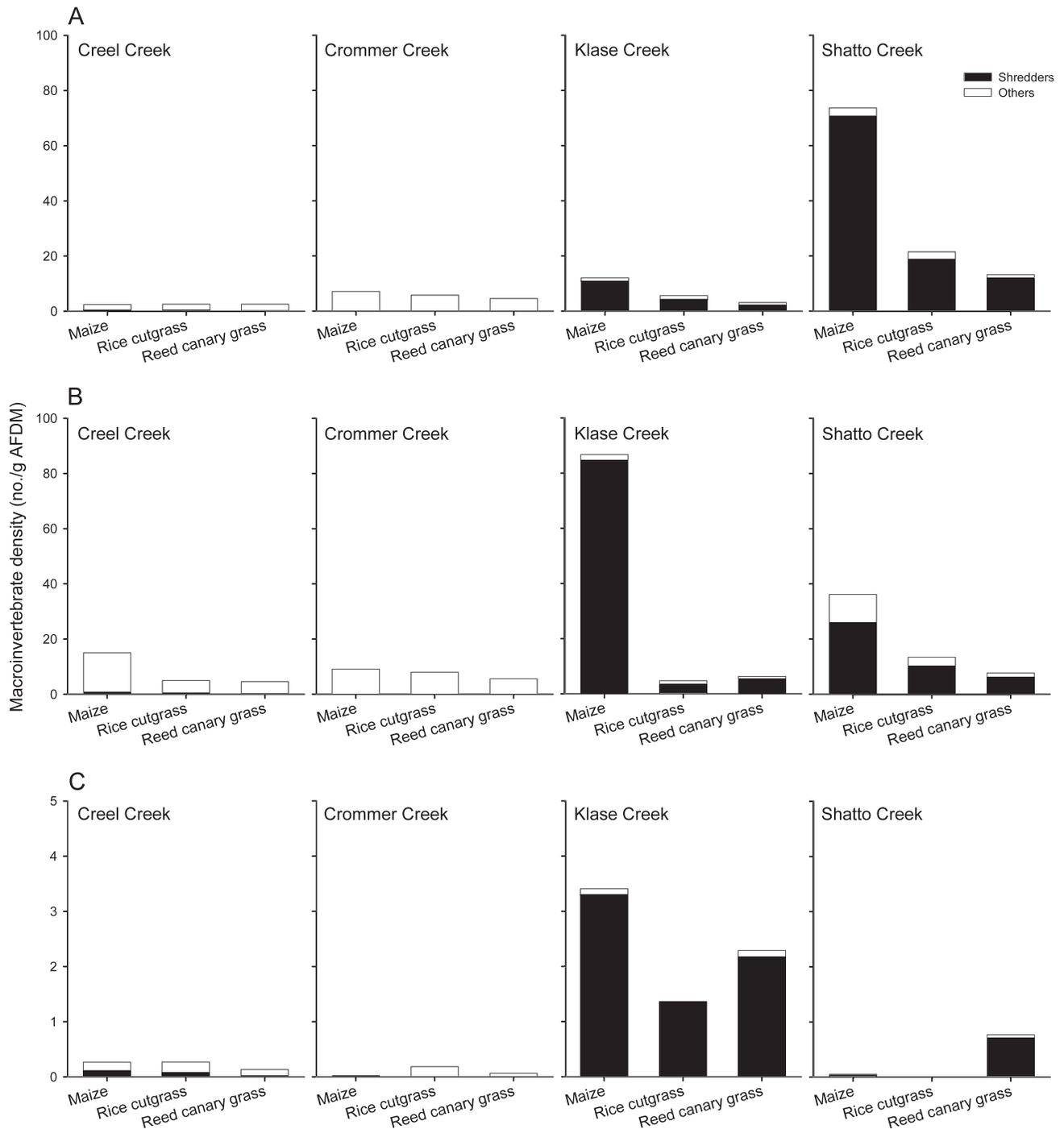
FIG. 5.   Mean density of shredding and other (nonshredding) macroinvertebrates (no./g ash-free dry mass [AFDM]) on maize, rice cutgrass, and reed canary grass litterbags in the stream channels of the 4 study streams on day 15 (A) and day 49 (B), and in the riparian habitats of the 4 study streams on day 15 (C). Note the different scale of the y-axis in each panel.

inundated longer than banks, whereas in Crommer Creek, banks were inundated longer than floodplains. Nevertheless, breakdown rates were not related to inundation duration in riparian habitats (ANCOVA, $F_{1,18} =1.4$, $p = 0.26$). Furthermore, breakdown rates in

riparian habitats were not related to the number of high-flow (storm) events (ANCOVA, $F_{1,6} =3.6$, $p = 0.10$), air temperature (ANCOVA, $F_{1,6} = 0.77$, $p = 0.41$), or shredder density on day 15 (ANCOVA, $F_{1,6} = 3.8$, $p = 0.10$).
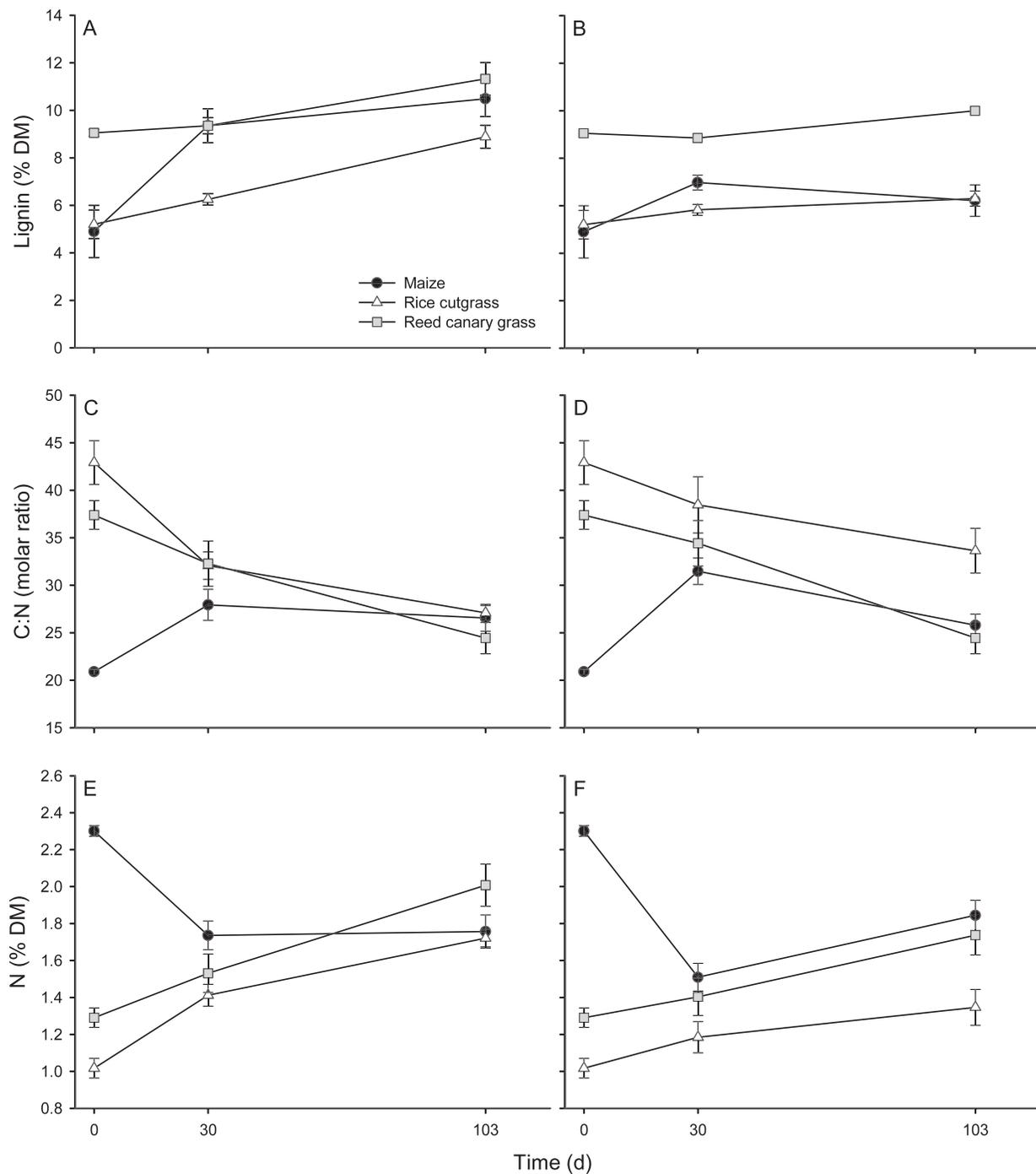
Fig. 6.   Mean (±1 SE) lignin (% dry mass [DM]) (A, B), C:N (molar ratio) (C, D), and N content (% DM) (E, F) of maize leaves, rice cutgrass, and reed canary grass in litterbags in the stream channels (A, C, E) and in the riparian habitats (B, D, F) over the decomposition period (days 0, 30, 103).

Intrinsic drivers of breakdown rates in stream and riparian habitats.—OM chemistry explained variation in breakdown rates among the 3 OM types. However, we did not explore these relationships in detail because sample sizes were small (n = 3). The strongest relationship observed was a negative relationship between breakdown rate and the ratio of initial % lignin to % N (simple linear regressions, stream: r^2 = 0.98, p = 0.09, riparian: r^2 = 0.99, p = 0.03).
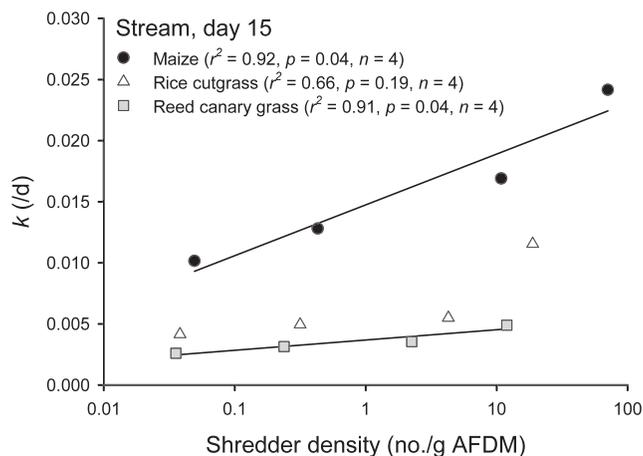
Fig. 7. Relationships between mean in-stream breakdown rate (k; /d) of maize leaves, rice cutgrass, and reed canary grass and mean shredder density (no./g ash-free dry mass [AFDM]) measured on litterbags in each stream on day 15 of the study.

Discussion

Decomposition of maize and grasses in agricultural streams

Headwater streams draining row-crop agriculture receive allochthonous inputs of maize detritus (Rosi-Marshall et al. 2007, Jensen et al. 2010) and grasses (Menninger and Palmer 2007), and breakdown rates of these OM types form a continuum similar to that described for forested (Petersen and Cummins 1974, Webster and Benfield 1986), tallgrass prairie (Smith 1986), and tropical (Ardón et al. 2009) streams. According to the classification scheme developed by Petersen and Cummins (1974; fast: $k > 0.01$/d, medium: $0.005 < k < 0.01$/d, slow: $k < 0.005$/d) for decomposing leaf species in aquatic ecosystems, maize decomposed at a fast rate in agricultural streams, rice cutgrass decomposed at a medium rate, and reed canary grass decomposed at a slow rate. In contrast, all OM types decomposed at a slow rate on the floodplains and banks, although maize decomposed faster than rice cutgrass and reed canary grass. Thus, in addition to a range of breakdown rates across 3 OM types, we also found a range of breakdown rates between stream and riparian habitats, as other investigators have reported for other streams and floodplains (Tiegs et al. 2007, Langhans et al. 2008, Harner et al. 2009). The range of breakdown rates measured in agricultural streams suggests that maize and grasses are available to heterotrophic consumers (microorganisms and invertebrates) for a long time.

Differences in breakdown rates among maize leaves, rice cutgrass, and reed canary grass may be the result of differences in tissue lignin and N content.

Lignin is a complex refractory compound that is resistant to microbial decay, whereas N is an essential nutrient for heterotrophic microorganisms, and both lignin (Melillo et al. 1984, Gessner and Chauvet 1994, Royer and Minshall 2001) and N content (Triska and Buckley 1978, Chadwick and Huryn 2003) are strong predictors of breakdown rates. We attribute the faster decomposition of maize leaves to higher initial N (2.30%) and lower initial lignin content (4.9%), whereas the lower N (1.29%) and higher lignin (9.1%) in reed canary grass resulted in slower decomposition rates. Rice cutgrass had a similar lignin content to maize (5.2%), but a lower N content (1.02%), and decomposed at an intermediate rate. Overall, the best predictor of breakdown rates among the 3 OM types was the ratio of initial lignin to N, a relationship that also explained variation in aquatic breakdown rates of 48 species of deciduous leaves (Ostrofsky 1997). In general, maize leaves and grasses had lower lignin and higher N contents than leaves from temperate-forest tree species (Ostrofsky 1997, Ardón et al. 2009). For example, lignin and N contents of 7 common riparian tree species in the southern Appalachian Mountains, North Carolina, USA, ranged from 8.4 to 21.1% and 0.32 to 1.24%, respectively (Ardón et al. 2009). Leaf shape and structure also may influence breakdown rates of maize leaves and grasses compared to many riparian tree species. Maize, rice cutgrass, and reed canary grass are monocots, and their parallel leaf venation may facilitate breakdown via fractionation and invertebrate feeding in comparison to leaves with branching venation (e.g., maple leaves). Overall, allochthonous detritus entering agricultural streams is a labile, high-quality substrate, especially in comparison to leaves that fall into temperate forested streams. Therefore, potential exists for rapid incorporation of this detrital material into agricultural stream food webs.

Despite its lability, agricultural detritus showed temporal trends in chemistry similar to those of decomposing leaf litter in temperate forested streams. Percent lignin in all 3 OM types increased through time, a result suggesting that labile compounds (e.g., cellulose, hemicellulose, lipids) were degraded in preference to lignin. The increase in % lignin was not as prominent in the riparian samples, a result reflecting slower breakdown rates. The % N in rice cutgrass and reed canary grass also increased over the decomposition period and probably reflected microbial immobilization of N and accumulation of microbial biomass through time (Kaushik and Hynes 1968, 1971, Suberkropp et al. 1976, Triska and Buckley 1978, Killingbeck et al. 1982). In contrast, % N in maize leaves initially decreased and then leveled off.

The decline probably reflected net detrital N lost via rapid mass loss of maize leaves, and the plateau probably reflected a net increase in microbial N through time.

Microbial decomposition by bacteria and fungi that colonize detrital material is an important component of OM processing, and the activity of microorganisms on decomposing litter tends to reflect litter quality (Canhoto and Graça 1996, Royer and Minshall 2001, Stelzer et al. 2003, Ardón et al. 2006). In our study, microbial respiration rates were higher on the low-lignin, high-N, fast-decomposing maize leaves than on the 2 grasses. However, microbial respiration rates on maize incubating in the stream channel were higher for only the first 30 d, and then were similar to rates on grasses for the rest of the study. In contrast, respiration rates on maize in riparian habitats were higher than rates on grasses throughout the study. This discrepancy is probably the result of rapid in-stream decomposition of maize leaves in Shatto Creek by shredders, which left little, primarily refractory (i.e., veins), detritus available to be colonized and respired after 30 d. In addition, microbial respiration rates were similar on OM in the riparian habitats and the stream channel. Microbial respiration incubations were done in stream water, a situation that simulated flooding of the riparian habitats. Thus, these results suggest that OM in the riparian habitats is primed for microbial activity once inundation occurs. Furthermore, decomposition in the riparian habitats probably was driven primarily by microbial consumption and leaching of soluble compounds (Molles et al. 1995) rather than by invertebrate consumption. Shredder density on day 15 was lower on litterbags in the riparian habitats than in the stream channels. Moreover, samples were collected during a high-flow event, so density probably was higher than if the litterbags had been collected when riparian habitats were not inundated. During these periods, we observed low densities of terrestrial detritivores on riparian litterbags. However, we did not focus on determining the extent to which terrestrial detritivores contributed to the decomposition of maize and grasses in riparian habitats.

Microorganisms are thought to be important in OM decomposition in agricultural stream channels (Hladyz et al. 2010) because shredder density and richness generally are low in agricultural streams (Benfield et al. 1977, Tuchman and King 1993, Huryn et al. 2002, Niyogi et al. 2003). However, in 2 of our 4 agricultural streams, shredders were very abundant and appeared to strongly control OM decomposition. Sixty-six to 92% of the variation in breakdown rates among streams could be explained by differences in the density of shredders in litterbags. Shredder density ranged from <1 to 85 individuals/g AFDM, which is a larger range than reported in other decomposition studies in agricultural streams (Niyogi et al. 2003, Hagen et al. 2006, Paul et al. 2006). The high density of shredders was primarily a result of the prevalence of isopods (*Caecidotea* and *Lirceus*) in Klase and Shatto Creeks. Aquatic isopods are found in a variety of aquatic habitats, including both pristine and impacted streams (Hatchett 1947, Williams 1976, Pennak 1989, Maltby 1991, Tuchman and King 1993). In our study, high shredder density was associated with warm stream water temperatures. The extent to which shredder density and water temperature interacted to influence breakdown rates is not clear because our study was not designed to assess the effects of multiple extrinsic drivers on breakdown rates. Furthermore, we do not know whether water temperature was correlated with other environmental factors, such as high Ca concentrations, dissolved solids (Reynoldson 1961), or pesticides, that could have influenced isopod distributions.

Shredders in temperate deciduous forested headwater streams rely on a pulsed input of allochthonous detritus in autumn (Cummins 1974, Cummins et al. 1989), but whether a similar reliance on allochthonous inputs occurs in agricultural streams in unknown. Grasses may provide a more temporally sustained and reliable resource to stream consumers than maize detritus because grasses tend to slump into streams and decompose while remaining rooted in the banks. Furthermore, grass material can be both live and dead (Menninger and Palmer 2007), and thus, may be available for decomposition year-round. In contrast, inputs of maize detritus can be sporadic (Rosi-Marshall et al. 2007, Jensen et al. 2010). Thus, maize may be an unreliable food source for microbial and macroinvertebrate consumers. The primary mechanism for delivering maize detritus into streams is overland flow associated with heavy rain or windstorms (Tank et al. 2010b), and peak inputs can occur several months after crop harvest (Jensen et al. 2010). The dominant shredders in the study streams were isopods, which are considered to be scavengers (Pennak 1989). Isopods probably do not rely only on allochthonous inputs of grasses and maize, but rather feed on any available OM (e.g., filamentous algae, fine organics on sediments).

Effect of the 2-stage restoration on OM decomposition

The link between floodplains and main-channel habitats is essential for lateral, reciprocal transfer of energy, nutrients, and organisms (Junk et al. 1989,

Tockner et al. 2000), and re-establishing connections between streams or rivers and their floodplains (Tockner et al. 1999, Ward et al. 1999, Buijse et al. 2002) is a goal of many river restoration projects (Bernhardt et al. 2005). The 2-stage restoration strategy being implemented in midwestern USA agricultural streams results in the creation of new floodplain habitat. However, we found that OM decomposed similarly on newly constructed floodplains and on the steep banks of trapezoidal agricultural streams.

We predicted that increased water-residence time on the floodplains would stimulate microbially mediated decomposition of OM. The floodplains of 3 of the 4 study streams were inundated for longer periods than the upstream banks, but OM breakdown rates were not related to inundation duration or the number of high-flow events. These results differ from those of several studies in which longer periods of inundation stimulated decomposition (Gurtz and Tate 1988, Langhans and Tockner 2006, Padial and Thomaz 2006). However, in our study, inundation periods of banks and floodplains ranged from 1 to 34% of the total decomposition period and were generally shorter than the experimentally manipulated inundation periods in the Tagliamento River in Italy (litterbags inundated for 0%, 33%, 66% and 100% of the 30-d study; Langhans and Tockner 2006) and in the Paraná River in Brazil (litterbags inundated for 0%, 50%, and 100% of the 113-d study; Padial and Thomaz 2006). In contrast, in a prairie stream in Kansas (USA), Gurtz and Tate (1988) found that breakdown rates measured along a transect from the stream channel to the top of the banks responded to small changes in inundation (litterbags inundated for 0.003–4% of the 274-d study). However, the authors suggested factors that varied along the transect, such as soil moisture, may have contributed to the measured differences in breakdown rates. In our study, environmental factors that differed among the 4 streams might have had a greater influence than inundation duration on breakdown rates. Differences in air temperature, shredder density, and the number of high-flow events did not predict riparian breakdown rates among the 4 streams, but other environmental variables that influence terrestrial breakdown rates, such as moisture and humidity (Meentemeyer 1978), may have explained some of this variation.

The study streams had been restored for different lengths of time (1–4 y) at the onset of our study, but this variation probably did not influence OM decomposition on the floodplains. We predicted that breakdown rates would increase on the floodplains because of increased water-residence time, which is influenced by floodplain morphology and the presence of vegetation.

The structure of the restored floodplains is not expected to change significantly over the first few years of restoration (Powell et al. 2007a), and all restored floodplains were vegetated with grasses at the time of our study. Further, most of our study took place in winter, and during periods of inundation, water in the riparian habitats occasionally froze, encasing litterbags in ice (NAG, personal observation). Thus, even though the riparian habitats were inundated, decomposition by microorganisms may have proceeded at a slow rate during this time.

Overall, we found no evidence that breakdown rates differed between the restored floodplain habitats and the steep banks that characterize most agricultural channels. However, the availability of OM for decomposition by heterotrophs depends not only on inputs, but also on retention within the stream channel (Webster et al. 1994, 1999), and we hypothesize that the floodplain habitats created in restored agricultural streams may promote retention of detritus during higher flows. If retention increases on the floodplains, then the potential exists for greater lateral exchange of energy and nutrients between floodplains and the stream channel. However, this hypothesis remains to be tested. The primary intent of this restoration strategy was to increase channel stability. However, any additional improvement in the ecological function of the floodplains, such as increased biological removal of dissolved N via denitrification (Roley et al. 2012) or increased retention and processing of OM, may result in improved ecosystem services provided by these human-impacted streams.

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