Agricultural land use alters temporal dynamics and the composition of organic matter in temperate headwater streams

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Abstract: Intensification of agricultural land use leads to riparian clear cutting, which disrupts stream aquatic-terrestrial linkages through the loss of terrestrial particulate organic matter (POM). POM is important for structuring habitats and serves as a basal resource for food webs. We studied the effects of agricultural land use on the fate and temporal dynamics of POM inputs and standing crops by comparing 2 agricultural and 2 forested reference streams for 15 mo. We used the C spiraling metrics downstream velocity of organic C (V_{OC}) and index of retention (IR) to integrate information on the dynamics of benthic organic matter (BOM) with physical characteristics of the streams. Daily POM inputs into reference streams were 15 to 39 times higher than inputs into agricultural streams, and mean standing crops of total BOM were significantly lower in agricultural streams than in reference streams. Agricultural streams had significantly higher standing crops of fine benthic organic matter (FBOM), but 1.8 to 3 times lower coarse benthic organic matter (CBOM) than reference streams. The temporal dynamics of BOM standing crops differed between land use types. BOM varied seasonally in reference streams but varied stochastically over time in agricultural streams. V_{OC} was significantly faster and IR was significantly lower in agricultural than in reference streams. Further, V_{OC} was mainly determined by benthic organic carbon (BOC) and transported organic carbon (TOC). Analyses of BOM and carbon spiraling metrics suggested that reference streams were more retentive because of terrestrial POM inputs and higher habitat complexity, whereas high discharge and hydrological variability limited the retentive capacity of the agricultural headwaters. However, total litter decomposition rates were high in agricultural streams. Our use of spiraling metrics to integrate physical stream characteristics with temporal dynamics of BOM provides a mechanistic understanding of how agricultural land use affects POM dynamics in temperate headwaters and highlights the importance of natural riparian vegetation to restoration efforts. This understanding

is important in light of the growing concerns about the effects of intensive agriculture on stream ecosystems.

Key words: aquatic-terrestrial coupling, agriculture, organic matter, organic carbon spiraling, retention

Stream ecosystems, particularly forested headwaters, are tightly linked to their catchments by inputs of terrestrial particulate organic matter (POM) and dissolved organic matter. These inputs are seasonal in temperate deciduous forest streams, and most POM enters streams in autumn (Benfield 1997, Richardson et al. 2009, Tank et al. 2010). Terrestrial POM is an important trophic resource for secondary production (Wallace et al. 1997, Webster and Meyer 1997, Hall et al. 2000), and higher POM detrital storage, along with the habitat heterogeneity it creates, increases macroinvertebrate densities (Dobson and Hildrew 1992, Negishi and Richardson 2003).

The quantity and fate of POM is ultimately affected by how much POM is retained on the bottom of a stream reach (retention), which in turn depends on physical and biological stream characteristics such as in-stream complexity, POM decomposition, and POM transport (Webster et al. 1999). Several studies have shown that woody debris and logs increase in-stream structural complexity (e.g. Bilby 1981, Diez et al. 2000, Gurnell et al. 2005) and consequently retention (Webster et al. 1994, Pretty and Dobson 2004, Eggert et al. 2012). Trapped POM decomposes, which is the dominant process by which headwater streams lose POM (Richardson et al. 2009). However, discharge also strongly influences POM transport (Fisher and Likens 1972, Richardson 1992), and during storm flows increased discharge can contribute up to 75% of total annual POM transport in headwater streams (Webster et al. 1990).

The quality and quantity of POM are dependent on catchment land use. Several studies found that the inputs and standing crops of POM were lower in agricultural streams than in forested streams (Delong and Brusven 1993, 1994, Griffiths et al. 2012). These lower POM quantities were mostly a result of land use alterations, such as riparian clear-cutting, siltation, erosion, and altered hydrodynamics (Allan 2004, Blann et al. 2009, Gücker et al. 2009). Agricultural streams are often channelized and exhibit high hydrological variability (Moore and Wondzell 2005, O'Connell et al. 2007) with higher frequencies and magnitudes of floods, as well as altered timing of the flow regime. Hydrological alterations may alter the retentiveness of agricultural streams (Griffiths et al. 2012), but little is known about how hydrological events affect the quantitative and qualitative properties of POM standing crops in agricultural streams.

Assessing the different fractions of organic matter (OM) standing crops and inputs provides information about the structural and compositional properties of POM dynamics. However, understanding whole-system POM processing and fluxes is only possible by combining information about POM standing crops with physical and hydrological characteristics of streams, which can be done with spiraling metrics. Spiraling metrics are integrative measures of C transport, processing, and retention across stream reaches and catchments (Newbold et al. 1982, Minshall et al. 1992). These metrics include the organic C turnover rate (K_{OC}), the downstream velocity of organic C (V_{OC}), the organic C turnover length (S_{OC}) as the ratio of V_{OC} to K_{OC}, and the index of retention (IR) as the ratio of mean flow velocity to V_{OC}.

C spiraling metrics have been used to examine whole-stream C dynamics in agricultural streams (Griffiths et al. 2012, Thomas et al. 2005) and in forested reference settings (Minshall et al. 1983, 1992, Webster and Meyer 1997). A previous study suggested that the downstream transport of organic C is the main process in agricultural streams, primarily because of higher hydrological variability in impacted stream channels (Griffiths et al. 2012). The only study that has examined an organic C spiraling metric (S_{OC}) in reference and agricultural streams concurrently (Young and Huryn 1999) found higher values of S_{OC} at pasture sites than at naturally forested sites, which suggests that agricultural sites retain and process OM less efficiently.

Litter decomposition, the physical and biological processing of retained POM, is both a major pathway of POM loss from streams and a key ecosystem function of streams. However, litter decomposition is highly susceptible to catchment land-use alterations. Mesocosm experiments that simulate agricultural stressors have demonstrated increased litter decomposition rates with increasing nutrient concentrations and temperatures (Piggot et al. 2015).

The combined assessment of POM standing crops, inputs, processing, and transport can provide a more complete understanding of how land use affects stream POM dynamics. However, relatively little research has combined these characteristics of POM dynamics within 1 comprehensive study (but see Griffiths et al. 2012 for agricultural streams). Here, we compare POM composition, temporal dynamics, and functional retention measures between land-use types to understand the drivers of agricultural land use on stream OM dynamics and address the following hypotheses: 1) agricultural streams lack inputs from surrounding riparian vegetation, so they will have lower complexity, altered hydrology, and lower standing crops of POM than reference streams, 2) agricultural streams have increased hydrological variability and human land use practices, which will cause temporal patterns of POM input and BOM abundance to differ between reference and agricultural streams, and 3) agricultural streams have altered hydrological conditions, lower POM inputs, and fewer retentive structures and will therefore retain POM less efficiently than reference streams.

METHODS

Study sites

The study was conducted in 2 reference (Ochsenbach and Wormsgraben) and 2 agricultural (Sauerbach and Getel) headwater streams in the Harz Mountains, Germany (Figs 1, S1). The reference streams were located in pristine, deciduous forest catchments with low nutrient concentrations (Table 1). The agricultural streams were located in catchments dominated by agricultural and urban land use as evaluated by analyses of color infrared digital aerial photography (Arc Hydro, incorporated in ArcGIS 10.0; ESRI 2010, Redlands, USA). The catchment land use around the agricultural streams was arable land that primarily consisted of maize crop. This land-use type surrounded the study reaches of the agricultural streams for a minimum of 1.5 km upstream. The agricultural streams also lacked riparian trees and shrub vegetation, and any riparian vegetation was limited to 1–2 m buffer strips of herbaceous vegetation and grasses. The riparian vegetation along the agricultural streams was mowed in July-August of each year. The agricultural streams were incised and channelized, and they exhibited significantly higher nutrient concentrations than the reference streams (Table 1).

One agricultural stream (Getel) received discharge from a wastewater treatment plant (WWTP; mean population equivalent = 6833) ~4 km upstream of the study reach. However, the water conditions upstream and downstream of the WWTP were not significantly different, so effluents from the treatment plant did not appear to increase stream water inorganic nutrient and seston POM concentrations (Table S1).

Sampling of POM inputs and standing crops

We installed three 10-m longitudinal transects every 150 to 200 m in each stream to capture the spatial variability of the inputs and standing crops of POM in each study reach. We quantified POM inputs with a total of 6 lateral traps and 3 vertical traps in each stream reach (2 lateral and 1 vertical litter trap in each transect). Vertical traps had an opening of 1 m^2 covered with 1-cm mesh and were fixed at a height of ~1.5 m above stream level. We did not install vertical traps in agricultural streams because there were no trees. Lateral traps (1-cm^2 mesh) were anchored at the stream margins and were 1 m long, 20 cm high, and 30 cm deep with foil-lined bottoms. We emptied each trap monthly from October 2012 to March 2014 and froze the samples for later processing.

We estimated the standing crops of BOM monthly from October 2012 to November 2013 by mapping the proportion of the following mineral benthic substrates in each transect: megalithal (>40 cm), macrolithal (>20–40 cm), mesolithal (>6–20 cm), microlithal (>2–6 cm), akal (>0.2–2 cm), psammal (>6 µm–2 mm), and argyllal (<6 µm). We also mapped the proportion of the biotic habitat covered by the categories filamentous algae, submerged or emergent macrophytes, xylal (wood), roots, CPOM, and FPOM (AQEM Consortium 2002). We calculated average transect grain size (cm) as the weighted average of the mineral size fractions we found during habitat mapping. We then took 3 BOM samples that reflected the proportion of each substrate type per transect with a modified Surber sampler (55-µm mesh, area 0.0225 m^2) by slowly stirring the benthos up to a sediment depth of ~10 cm. BOM samples were stored in plastic containers and frozen until further processing.

OM sample processing

Size fractions of POM can differ between agricultural and reference streams. For example, FPOM in reference streams is mostly a product of the biological and physical processing of coarse particulate organic matter (CPOM) (Ward 1986), whereas FPOM in agricultural streams often originates from soil (Gurtz et al. 1980). Thus, in the laboratory, we sorted POM input samples into the categories leaves, wood, fruit, herbaceous vegetation, and miscellaneous CPOM. We calculated the monthly lateral inputs at each site per unit of stream surface area by combining inputs of both lateral traps and dividing POM input quantity by the length of the stream margin covered by both traps (2 m) and by average stream width (Menninger and Palmer 2007). BOM samples were categorized into fine (<0.2 mm; FBOM), medium (0.2–2 mm; MBOM), and coarse fractions (>2 mm; CBOM) with sieves. BOM particles >6 mm were manually sorted into the same categories as the POM inputs.

Each BOM and POM category was dried at 60°C for 24 h, weighed, and combusted in a muffle furnace at 540°C for 4 h to determine ash free dry mass (AFDM). We calculated the mineral fraction of FBOM as the proportion of mineral mass (difference between dry mass and AFDM) to the total sample dry mass. This calculation estimated the contribution of agricultural soils in benthic samples based on to the assumption that soil input to streams would be reflected in a higher proportion of the mineral fraction. POM input units are g AFDM m^{-2} mo^{-1} and BOM values are the average of the 3 transects in g AFDM/m^2.

Physical and chemical stream characteristics

To monitor and link physical and chemical stream characteristics (Table 1) to BOM dynamics, we measured stream water dissolved oxygen, temperature, specific conductivity, and pH every 15 min from October 2012 to November 2013 with multiparameter probes (YSI EXO2, Yellow Springs Instruments, Yellow Springs, USA). We also used standard methods (Kamjunke et al. 2013) to measure nutrient concentrations (NO_3-N, NO_2-N, NH_4-N, dissolved organic N (DON), total dissolved N (TDN), soluble reactive P (SRP), total P (TP), dissolved organic C (DOC), and particulate organic C (POC) from water samples we took monthly from each stream. We recorded water pressure (corrected for atmospheric pressure) every 15 min with pressure loggers (Synotech HOBO, Hückelhoven, Germany) and calculated water depth from corrected pressure measurements. We established stage-discharge relationships based on repeated slug injections of salt solutions we did during variable discharge (Q) conditions from August 2012 to December 2013 (see Fig. S2 for discharge measurements over the sampling period). We estimated average flow velocity by dividing Q by the width and depth of the stream during salt addition experiments. Hydrological variability was calculated as the ratio between maximum and mean water depth. The slope of the stream reach was measured with a Leica NA 724 (Leica Geosystems, Munich, Germany).

C spiraling metrics

We used C spiraling metrics to characterize organic C (OC) transport and retention processes by combining hydrological and physical data with measurements of BOM dynamics. We used data from between October 2012 and November 2013. We calculated V_{OC} (m/d) and IR (dimensionless) following Newbold et al. (1982) and Minshall et al. (1992):

$$V_{OC} = \frac{TOC\ x\ Q}{BOC\ x\ w} \qquad \text{Eq. 1}$$

$$IR = \frac{v_{wat}}{V_{OC}} \qquad \text{Eq. 2}$$

where TOC = total transported OC concentration (g C/m^3), Q = discharge (m^3/d), BOC = total benthic OC (g C/m^2), w = mean stream width (m), and v_{wat} = mean flow velocity (m/d). Low IR values indicate that streams transport OC at the same rate as water flows downstream, whereas high values mean that streams retain C well (Minshall et al. 1992). We converted BOM to C units with a 48.4% conversion (Thomas et al. 2005). Our study focused on the particulate C pathway, so we did not include measures of DOC in the TOC compartment. Hence, our values of TOC are based on monthly measurements of POC.

Litter decomposition

We compared litter decomposition rates between land use types to relate findings to standing crops and dynamics of BOM in respective streams. Litter decomposition was measured from October 2014 to January 2015 after BOM and POM input samples were taken. The 4 streams did not undergo any obvious changes in physical or chemical characteristics after we sampled BOM and POM inputs and started the decomposition experiment, but we monitored stream water to assess if physical and chemical conditions changed during the litter decomposition experiment. We sampled water chemistry bi-weekly, recorded water temperature and level continuously, and analyzed these metrics as described above.

To quantify litter decomposition we anchored a total of 14 fine-mesh (40 μm) and 14 coarse-mesh (4 mm) bags to the central streambed of each stream. Macroinvertebrates had access to the coarse-mesh bags but not the fine-mesh bags, so we quantified microbial litter decomposition with the fine-mesh bags, and total litter decomposition rates with the coarse-mesh bags. Each mesh bag was filled with 4 to 5 g of freshly fallen alder leaves (*Alnus glutinosa*, L.) that had been dried at 60 °C for 14 h. Four bags per mesh size were retrieved after 2, 4, and 10 w. Bags that were physically damaged were discarded from analyses. Surplus bags were used as substitutes when bags went missing or became damaged, and all remaining bags were retrieved in the final sampling after 10 w. There were enough bags that we obtained at least 3 replicates from each sampling time. However, the 10-w sample bags from one of the reference streams (Wormsgraben) were lost because of high discharge in early January.

In the laboratory, leaves were rinsed, dried at 60 °C for 24 h, and weighed to the nearest 1 mg. We determined AFDM as described above. Microbial (k_{micro}) and total (k_{total}) decomposition rates were calculated according to a standard exponential breakdown model (Petersen and Cummins 1974):

$$m_t = m_0 \times e^{-kt} \qquad \text{Eq. 3}$$

where m_t is g AFDM remaining at time *t* in days, m_0 is g AFDM at the start of the experiment, and k (d^{-1}) is the decomposition rate coefficient.

We also calculated temperature-corrected *k* with degree-days at time *t* by summing the average temperature per d for each day the leaves were in the water. We calculated litter decomposition rates with and without a temperature correction because agricultural streams are often warmer than forested streams and correcting for temperature would remove the effect of this land-use associated variable. However, the temperature correction did not change the decomposition rates, so we used the rates without the temperature correction in further analyses.

To explore the contribution of macroinvertebrate shredders to leaf litter processing in the 4 streams, macroinvertebrates were collected from the bags during each sampling, preserved in 96% ethanol, and identified to family level. Macroinvertebrates were assigned to functional feeding groups according to the AQEM/STAR ecological river classification system (Schmidt-Kloiber et al. 2006).

Data analyses

We used generalized additive models (GAMs) to test our 1st hypothesis that POM inputs and BOM standing crops differed between land use types. We used the function *gam* in the R package *mgcv* to build these models (Wood 2011; R Development Core Team 2016). We used GAMs because they can model variation in data structures that have complex non-linear relationships with the response variable (Wood 2006, Zuur et al. 2009). We linked the response variables to the categorical fixed factor stream nested within the factor land use. To account for temporal dependency between monthly measurements of response variables, we added smoothing terms to model the temporal pattern of these response variables. These were calculated as interaction terms between land use type and sampling date with the 'by' command. We used the R package *itsadug* (van Rij et al. 2016) to add a correlation structure to the model to account for temporal autocorrelation between replicates of response variables. Models were built based on gamma distributions with a log-link function. We used the function *gam.check* in the R package *mgcv* to visually evaluate the normalized residuals of these fitted models in terms of normality of errors and homogeneity of variance. We also used the GAM approach to test for significant differences between land use types for the following response variables: environmental parameters, organic C spiraling metrics, and litter decomposition rates.

To test our 2nd hypothesis that temporal patterns of POM inputs and BOM standing crops differed between land-use types, we used GAMs and the previously described interaction term between land use type and sampling date. A significant interaction between sampling date and land use type indicated a significant difference between the temporal dynamics of reference and agricultural streams. Smoothing terms from GAM analyses were significant at $\alpha = 0.01$ because of the higher uncertainty associated with *p*-values from these terms (Wood 2006).

There is no statistical approach available to calculate pairwise comparisons from a GAM model, so we used generalized linear mixed models (GLMM) (Bates et al. 2015) to test for significant differences between the 4 individual streams with the *glmer* function from the R package *lme4*. This model included stream as the fixed factor as well as random slope and intercept terms that allowed the coefficients of the temporal variable sampling time (monthly replicates to vary by stream to adjust for temporal replication in the model. Subsequent pairwise comparisons of streams were done with the function *lsmeans* in the R package *lsmeans*. The R code we used for these models is available on github and zenodo (https://github.com/ROMYWILD/R-script-GAM-Organic-matter-dynamics/tree/v2; doi: 10.5281/zenodo.1409618).

To address our 3rd hypothesis we used 2 approaches to identify potential drivers of differing retentiveness between agricultural and reference streams. The 1st approach determined which of the input variables (Q, BOC, TOC) were associated with the composite metrics V_{OC} and IR. We constructed stream-specific generalized linear models (GLM) that related the variables Q, TOC, BOC, flow velocity, and the interactions between Q and BOC and Q and TOC to the response variable V_{OC}. IR is the ratio between V_{OC} and flow velocity, so we analyzed the relationship between IR, V_{OC}, and velocity with a 2nd set of GLMs. We did not include stream width in this analysis because measurements of stream width were too infrequent.

The 2nd approach assessed how hydrological and physical variables affected the standing crops of different categories of BOC and BOM (FBOM, MBOM, and CBOM) by relating these variables to stream retentiveness with GLMs. The variables we used to describe stream retentiveness were discharge (Q), hydrological variability as the ratio between maximum water level and mean water level, wood BOM as a measure of structural complexity, and POM inputs. Wood BOM is part of the CBOM compartment, so we excluded wood BOM from CBOM for this analysis. We tested for collinearity between predictor variables with Pearson correlations, and found that no variable pairs had correlation coefficients of $r > 0.3$.

We then tested the effect of shredder abundance on leaf litter decomposition with Pearson correlations between the cumulative abundance of shredders and percentage loss of AFDM in coarse mesh bags. We used AFDM loss as the dependent variable because the leaf litter bags lost up to 80% of their content in the first 2 wk, which meant the litter decomposition rate could not be accurately estimated for the remaining duration of the experiment. We analyzed total invertebrate shredding activity by calculating the cumulative abundance of macroinvertebrate shredders by adding the mean abundance of shredders detected in samples after 2 and 4 w to abundances detected in samples after 4 and 10 w.

All statistical analyses were done with R (v.3.3.2, R Development Core Team 2016, Vienna, Austria).

RESULTS

Organic matter inputs

Agricultural streams had significantly lower total POM inputs than reference streams (GAM: t = -15.68, p < 0.001). The mean (± SD) POM inputs were 0.1 ± 0.1 g AFDM m^{-2} d^{-1} into agricultural streams and 1.3 ± 1.3 g AFDM m^{-2} d^{-1} into reference streams. Lateral POM inputs into reference streams were 0.4 ± 0.6 g AFDM m^{-2} d^{-1}, and we assumed that there were no vertical litter inputs to agricultural streams because there was no forest canopy. There was a significant interaction between sampling date and land use type that indicated a significant effect of agriculture on temporal POM input patterns (GAM: t = 5.25, p < 0.001). Leaves dominated inputs into reference streams in autumn, whereas herbaceous vegetation dominated inputs into agricultural streams throughout the year (Fig. 2). Inputs of herbaceous vegetation were significantly higher in agricultural than in reference streams (Table 2) and peaked in the 2 agricultural streams in July (Sauerbach: 0.2 ± 0.1 g AFDM m^{-2} d^{-1}) and August (Getel: 0.3 ± 0.1 g AFDM m^{-2} d^{-1}).

Benthic organic matter

Agricultural streams had significantly lower mean monthly total BOM, MBOM, and CBOM standing crops than reference streams (Table 3, Fig. 3), but agricultural streams had significantly higher mean FBOM standing crops than reference streams (Table 3, Fig. 3). However, FBOM standing crops varied within land use categories (Table 3). The mineral fraction of fine benthic matter in monthly samples was significantly higher (GAM: t =16.66, p < 0.001) in agricultural (92 ± 3%, mean ± SD) than in reference streams (77 ± 8%).

Temporal dynamics of FBOM and MBOM differed significantly between reference and agricultural streams (FBOM: GAM, F = 6.58, p < 0.001; MBOM: GAM, F = 7.29, p < 0.001; Fig. 5). In the reference streams, FBOM and MBOM were highest in autumn, whereas in agricultural streams, FBOM and MBOM standing crops were highest in winter and spring (Fig. 4).

Mean monthly CBOM and its fractions of wood, fruit, leaves, and CPOM were significantly higher in reference than in agricultural streams (Fig. 4, summary statistics in Table 3). In contrast, the contribution of herbaceous vegetation to CBOM was significantly higher in agricultural than in reference streams. The temporal pattern of CBOM standing crops differed between land use types (GAM, $F = 6.13$, $p < 0.001$; Fig. 5). In reference streams, CBOM standing crops were highest during autumn and winter, whereas CBOM in agricultural streams peaked February–March and July–August. The percentage of herbaceous vegetation that entered the agricultural streams because of stream margin mowing in July and August was 28% of the total yearly herbaceous vegetation standing crop and 20% of total CBOM standing crop. These elevated standing crops of herbaceous vegetation in agricultural streams were detectable for 2 mo before they returned to background levels (Fig. 4).

Organic matter retention

Mean monthly V_{OC} was an order of magnitude higher in agricultural than in reference streams (GAM, $t = 7.72$, $p < 0.001$) (Fig. 6), but the temporal dynamics of V_{OC} did not differ significantly between reference and agricultural streams (GAM, $t = 1.28$, $p = 0.24$). The highest values of V_{OC} were found in early and late spring in both land use types, and V_{OC} was lower in autumn in reference streams but not in agricultural streams (Fig. S3)

However, there was high variability between streams of the same land use type, and V_{OC} averaged 6 ± 9 m/d (mean ± SD) and 31± 90 m/d in the forested streams Ochsenbach and Wormsgraben, respectively. V_{OC} values in the agricultural stream Sauerbach (30 ± 26 m/d) were 6-fold lower than those in the agricultural stream Getel (194 ± 358 m/d; Fig. 6). GLM analyses showed that BOC was the strongest predictor of V_{OC} in both agricultural streams (Sauerbach: t = -4.4, p < 0.001; Getel: t = -5.0, p < 0.001) and in the reference stream Ochsenbach (t = -4.5, p < 0.001) (Table 4, Table S2). Discharge was strongly positively related to V_{OC} in the reference stream Wormsgraben (t = 5.0, p < 0.001) and to a lesser degree in the agricultural streams Sauerbach (t = 3.5, p = 0.001) and Getel (t = 2.5, p = 0.02). In contrast, TOC was positively associated with V_{OC} only in the agricultural streams (Sauerbach: t = 3.7, p = 0.001; Getel: t = 5.2, p < 0.001) (Table 5, Table S2).

The IR, a measure of the balance between POM transport and storage, was significantly higher in reference than in agricultural streams (GAM, t = -8.77, p < 0.001; Fig. 6). IR was highest in the reference streams (Wormsgraben = 2184 ± 3004, mean ± SD and Ochsenbach = 1524 ± 1383), and lower in the agricultural streams (Sauerbach = 706 ± 657 and Getel = 342 ± 273). There were no significant differences in temporal patterns of IR between land use types (GAM, t = 1.34, p = 0.32). Seasonal patterns of IR were similar to those of V_{OC} (Fig. S3). Dynamics of IR were not significantly related to any input variables but V_{OC} (Ochsenbach: t = -5.8, p < 0.001; Wormsgraben: t = -4.7, p < 0.001; Sauerbach: t = -10.0, p < 0.001, Getel: t = -8.7, p < 0.001), except for the reference stream Wormsgraben, where IR was also significantly negatively related to flow velocity (t = -2.9, p = 0.006) (Table S2).

Environmental drivers of BOM dynamics

FBOM and MBOM standing crops were inversely related to hydrological variability in the agricultural stream Sauerbach (FBOM: t = -3.0, p = 0.004; MBOM: t = -3.4, p < 0.001) and positively related to discharge in the agricultural stream Getel (FBOM: t = 5.3, p < 0.001; MBOM: t = 5.2, p < 0.001) (Tables 4, S3). In contrast, discharge in the reference streams was negatively related with FBOM in the Wormsgraben (t = -3.0, p = 0.004). The amount of wood in the reference stream Wormsgraben was positively related to the standing crops of FBOM (t = 3.7, p < 0.001), MBOM (t = 5.1, p < 0.001), and CBOM (t = 4.8, p < 0.001). The standing crop of wood was positively associated with CBOM in the reference stream Ochsenbach (t = 2.9, p = 0.006) and in the agricultural stream Getel (t = 2.5, p = 0.02) (Table 4, Table S3). Additionally, we found a significant positive effect of POM inputs on MBOM (t = 3.4, p = 0.002) and CBOM (t = 2.7, p = 0.009) in the reference stream Wormsgraben, and a marginally positive effect of POM inputs on CBOM in the agricultural stream Getel (t = 2.2, p = 0.03) (Tables 4, S3).

Leaf litter decomposition

Total litter decomposition rates (k_{total}) and the loss of AFDM (%) in coarse mesh bags were significantly higher in agricultural than in reference streams (GAM k_{total}: t = -3.85, p < 0.001; GAM AFDM loss: t = 3.78, p < 0.001), but rates varied within land use types (Fig. 7). In contrast, microbial decomposition rates (k_{micro}) did not differ between land use types (GAM, t = 1.02, p = 0.31) (Fig. 7). The loss of AFDM (%) in coarse mesh bags was positively correlated with the cumulative number of macroinvertebrate shredders in both reference streams (Pearson correlation: r = 0.81, p < 0.001) and agricultural streams (r = 0.73, p < 0.001) (Fig. S4). *Gammarus pulex* was the dominant shredder in the reference stream Ochsenbach (40% of total abundance) and in the agricultural streams Sauerbach (80%) and Getel (74%). Limnephilidae (Trichoptera) (44%) and *Nemoura* sp. (Plecoptera) (31%) were the dominant shredders in the reference stream Wormsgraben.

DISCUSSION

Effects of agricultural land use on POM inputs and BOM dynamics

Human driven alterations of catchment land use can profoundly affect how streams interact with their terrestrial surroundings. In this study we showed that agricultural land use around streams decreases POM inputs relative to streams surrounded by forested land. Total POM inputs were significantly lower in agricultural than in reference streams because of the absence of riparian trees. This result is similar to the findings of Delong and Brusven (1994) and Benfield (1997). Our results are also similar to other studies that analyzed POM inputs to streams with either agricultural or reference backgrounds. The mean total inputs to our reference streams (499 ± 206 [mean ± SD] g AFDM m^{-2} y^{-1}) were similar to the total inputs (629 g AFDM m^{-2} y^{-1}) to a 1^{st}-order reference stream in North Carolina (Satellite Branch; Wallace et al. 1995). Our results were also similar to various other 1^{st}-order reference streams with mixed deciduous forest vegetation in the US, Germany, and Canada that had total POM inputs ranging from 448 to 761 g AFDM m^{-2} y^{-1} (Benfield 1997). The lateral inputs (24 ± 4.3 g AFDM m^{-2} y^{-1}) into our agricultural streams from herbaceous riparian vegetation were lower than inputs into a 1^{st}-order agricultural stream section in Lapwai Creek (Idaho) that had direct litterfall inputs from herbaceous and shrub vegetation of ~47 g AFDM m^{-2} y^{-1} (Delong and Brusven 1994).

The significantly higher total BOM, particularly CBOM, standing crops in our reference streams relative to the agricultural streams is the result of the lack of riparian trees along agricultural streams. The quantity of total BOM in our reference streams was similar to the quantity in forested reference streams in North America (Fig. 8). In contrast, the mean total BOM and FBOM in our agricultural streams, especially Sauerbach, were in the upper range of reported values compared with agricultural streams of the US Midwest (Griffiths et al. 2012) and Lapwai Creek in Idaho (Delong and Brusven 1994) (Fig. 8, Table S4). In the forested reference streams, the high total BOM standing crops mostly resulted from higher CBOM standing crops, but the high total BOM in the agricultural streams resulted from high FBOM storage (Fig. 8, Table S4).

Thus, FBOM in our reference streams was probably a product of the CBOM fraction, and primarily derived from riparian POM inputs. The high organic and low mineral fraction of FBOM in reference streams supports the idea that FBOM primarily originates from processed riparian POM in reference streams. However, the 2 reference streams had very different FBOM and MBOM standing crops, which is contrary to the expectation that higher inputs from riparian vegetation would result in higher standing crops of FBOM. We found a strong negative relationship between FBOM and discharge in the Wormsgraben, the reference stream with lower FBOM and MBOM. The Wormsgraben stream bed had a steeper slope and higher discharge, which probably caused it to have a lower storage capacity of FBOM and MBOM than the other reference stream.

The high FBOM standing crop in the agricultural stream Sauerbach may be the result of soil erosion and stream bank failure. We were unable to measure erosional inputs with lateral traps, but we did observe bank failure and erosion from agricultural fields in other stream sections during field sampling that suggested inputs of FBOM from bank failure are localized in these agricultural systems. Moreover, we found that fine benthic matter in agricultural streams had a higher mineral content than in reference streams. Intensively farmed soils usually have higher mineral contents, whereas FBOM in forested headwater streams usually has higher organic content because it is mostly a product of physical and biological POM processing. Thus, this result suggests that large amounts of agricultural soils wash into agricultural streams. Bank erosion and failure are the main sources of FBOM in agricultural and prairie streams (Winterbourne et al. 1981, Laubel et al. 2003), and erosion has caused high FBOM standing crops in a stream in a logged catchment (Golladay et al. 1989). FBOM standing crops were similar in streams of the 2 land use types on a quantitative base, but qualitative differences (mineral/organic C content) clearly separated agricultural from forested reference streams and highlights the susceptibility of agricultural streams to stochastic increases of mineral fine sediment loads.

The high temporal variability in CBOM standing crops in the agricultural streams we studied was probably a result of riparian management practices rather than seasonal dynamics. The higher standing crops of herbaceous vegetation in summer were from stream margin mowing, which caused pulse inputs of this fraction in July and August. These temporarily high standing crops of herbaceous vegetation suggest that the lack of POM inputs from riparian tree vegetation in agricultural open-canopy systems can be partially compensated for by herbaceous vegetation growing along the stream channel (Menninger and Palmer 2007). Likewise, Griffiths et al. (2012) observed that herbaceous vegetation contributed 81 to 100% to CBOM pools in agricultural streams.

Organic matter retention

Agricultural streams retained significantly less OM than reference streams, as reflected by higher values of V_{OC} and lower values of IR. These results were driven primarily by the temporal dynamics of BOC, Q, and transported organic carbon (TOC) in agricultural streams. In contrast, Q (Wormsgraben) or BOC (Ochsenbach) were the most important environmental predictors of OM retention in the reference streams. Further, in reference streams wood and POM inputs from forest vegetation controlled standing crops of BOC, but in agricultural streams discharge and hydrological variability controlled the standing crops of BOC.

Together, these results suggest that OM retention differed between land use types because of the autumnal POM inputs in reference streams that considerably increased BOM standing crops throughout the year. Thus, the data support our hypothesis that the seasonal supply of POM and the presence of suitable in-stream structures such as woody debris are important for OM retention in headwater streams. This hypothesis was also supported by the significantly higher standing crop of wood BOM in reference streams than in agricultural streams. Further, the significant positive relationship between the quantity of wood and FBOM, MBOM, and CBOM, which we only found in reference streams, indicates that riparian wood enhances in-stream OM retention for all BOM categories. The presence of in-stream structures that retain BOM, such as woody debris, is particularly important in the light of the hydrological variability in these streams. Our results clearly show that OM retention differed markedly between agricultural and reference streams, even though discharge conditions were similar (e.g. Getel and Wormsgraben). For example, the reference stream Wormsgraben receives inputs from surrounding forest vegetation and therefore has higher structural complexity, which resulted in Wormsgraben retaining BOM even at moderate discharge levels and high flow velocities. Similarly, Minshall et al. (1992) found that high standing crops of BOC coincide with high flow velocities, which in turn led to high values of IR in a forested stream of a similar size. This observation suggests that the retentive effect of woody debris is strongest at high discharge levels. Similarly, Diez et al. (2000) and Koljonen (2012) found that a decrease in retention following the loss of wood and coarse woody debris was only large at high discharge levels, which highlights the importance of POM for structural retention in scenarios of increasing hydrological fluctuation.

Indeed, the agricultural streams in this study lacked CBOM, woody debris, and debris dams, which probably diminished their structural complexity (Webster et al. 1994) and reduced their BOM retention at higher discharge levels or during hydrological extremes (Bilby 1981, Gurtz et al. 1988, Gregory et al. 1991, Griffiths et al. 2009). The strong positive relationships between V_{OC} and TOC in both agricultural streams and the relationships between FBOM, MBOM, and discharge (Getel) and hydrological variability (Sauerbach) indicate that the discharge driven mobilization and transport of FBOM and MBOM strongly influence OM retention and C cycling in these streams. The reduction of FBOM standing crops and higher transport rates of POC may result from the high transport capacity of agricultural streams during high discharges and flow velocities (Jones and Smock 1991). Higher Q and flashier hydrographs are a consequence of agricultural land use, particularly in drained catchments (O'Connell et al. 2007, Blann et al. 2009). Thus, agricultural streams are more susceptible to flow-related loss of BOM than reference streams.

We used measures of POC as TOC in the calculation of V_{OC} and IR and probably missed the coarser fractions in transport because our POC measurements were based on point water samples. Up to 75% of POM can be exported from headwaters during spates (Webster et al. 1990) and these short-term events are rarely covered by regular sampling schemes. The smallest size class we analyzed is similar to the fraction of ultra-fine POM that has been observed as the main fraction in transport (84%) (Minshall et al. 1983). Thus, if we had been able to count the coarser fractions, our measurements of V_{OC} would probably be slightly higher and values of IR slightly lower.

OM processing

The high total decomposition rates in agricultural streams relative to those in reference streams indicated that POM is processed more efficiently in agricultural streams, which may facilitate its export from agricultural streams at high discharge. However, total decomposition rates were variable and context-dependent in our study. Similarly, Huryn et al. (2002) and Hagen et al. (2006) did not find clear land use induced patterns in litter decomposition rates. Our results contrast with previous studies, where canopy cover was positively correlated with litter decomposition (Voß et al. 2015)

The reason for the higher k_{total} in the agricultural stream Sauerbach than in the agricultural stream Getel and higher k_{total} in the reference stream Ochsenbach than in the reference stream Wormsgraben is probably the higher abundance of macroinvertebrate shredders, especially *G. pulex*, in Sauerbach and Ochsenbach. Benfield and Webster (1985) also found that shredder abundance controlled litter decomposition in pristine headwater streams. In studies in agricultural streams, Huryn et al. (2002) found a significant relationship between shredder biomass and leaf litter decomposition irrespective of land use type, whereas Niyogi et al. (2003) found no effect of shredder abundance and biomass on decomposition rates in agricultural streams. The observed higher k_{total} in agricultural streams may explain the high variability in the amount that herbaceous vegetation contributed to BOM in the agricultural streams, especially the rapid return to pre-mowing standing crops after the pulsed inputs we observed during summer months.

Microbial decomposition, however, did not differ between streams and land use categories, possibly as a result of the antagonistic responses of different agricultural stressors (Hagen et al. 2006). Eutrophication and higher temperatures could have led to an increase of k_{micro} in the agricultural streams (Gulis and Suberkropp 2003), but pesticides in both agricultural streams and contaminants from the wastewater treatment plant upstream of our sampling sites in the Getel probably adversely affected the microbial community, overriding the enhancing effect of nutrients (Rasmussen et al. 2012, Schäfer et al. 2012).

Ecosystem-level implications of altered OM dynamics

Our results highlight the utility of combining structural and functional analyses to study the complex effects of agriculture on POM dynamics in headwater streams. We demonstrated that the absence of terrestrial POM in agricultural streams probably affected standing crops of CBOM directly by reducing POM inputs and indirectly via the loss of retentive structures. The reduction of resource subsidies in agricultural streams appeared to be partially compensated by herbaceous vegetation inputs. However, univoltine macroinvertebrates, whose developmental cycles rely on seasonally predictable resource availability, might not be able to use these pulsed inputs efficiently. The altered temporal availability of POM in agricultural streams, particularly the absence of autumnal inputs of leaf litter, is concerning because macroinvertebrate consumers rely on litter subsidies from forest vegetation in winter (Junker and Cross 2014) and on retentive structures to keep these resources within the stream reach. These qualitative and temporal changes to resource subsidies in agricultural streams may change the trophodynamics of lotic food webs as communities adapt to the stochastic availability of POM. Further, changes in BOM quality, quantity, and temporal availability may have profound effects on microbially mediated ecosystem processes such as ecosystem respiration and nutrient retention (Stelzer et al. 2003, Tank et al. 2010), thereby affecting stream matter exports to downstream ecosystems and the atmosphere.

CONCLUSIONS

In conclusion, this study demonstrated profound effects of agricultural land use on seasonal POM dynamics of temperate headwater streams and highlighted potential implications for the consumer communities that depend on seasonally predictable POM availability. The stochastic variability of BOM dynamics and altered hydrology within the studied agricultural streams appears to limit the retentive capacity of these headwaters. Our results are consistent with the view that natural vegetated riparian zones are important for the structural and functional integrity of stream ecosystems and suggest that riparian zones in agriculturally impacted landscapes need to be developed and restored to maintain ecosystem functions. These measures could enable streams to return to more seasonal POM dynamics and enhance POM retention, thereby improving habitat conditions and resource availability for stream communities.

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Table 1. Characteristics of the study streams. Values of physiochemical variables are monthly means ± SD. TDN = Total dissolved nitrogen, DON = Dissolved organic nitrogen, TP = Total phosphorus, SRP= Soluble reactive phosphorus, DOC = Dissolved organic carbon, POC = Particulate organic carbon. Different lowercase letters indicate significant differences among the 4 streams as tested by generalized linear mixed models. GAMs were used to test for significant differences between the 2 land use types. Hydrological variability is expressed as the ratio between maximum and mean water depth. Significance levels are as follows: n.s = non significant, *** = $p < 0.01$.

	Reference		Agriculture		*t* for land use difference	
	Wormsgraben	Ochsenbach	Getel	Sauerbach		
Coordinates at transect start (lat and long)	51.773748 10.715571	51.734662 10.663493	51.757163 11.297438	51.720908 11.286528		
m a.s.l.	575	526	150	180		
Land use (%)						
Forest	95	76	32	35		
Arable	0	0	48	39		
Pasture	1	11	7	2		
Urban	0	9	11	22		
Bed slope (%)	4.9	1.5	0.6	0.6		
Width (m)	1.5 ± 0.4	1.0 ± 0.2	1.2 ± 0.2	1.0 ± 0.1		
Mean velocity (m/s)	0.1 ± 0.06	0.05 ± 0.01	0.26 ± 0.11	0.12 ± 0.01		
Discharge (L/s)	23 ± 15^{a}	13 ± 6^{b}	61 ± 33^{c}	19 ± 5^{a}	22.4	***
Hydrological variability	2.1 ± 0.6^{ac}	1.4 ± 0.2^{bd}	1.8 ± 0.8^{cd}	2.3 ± 1.1^{ab}	4.9	***
Mean grain size (cm)	5.7 ± 1.0^{a}	2.8 ± 1.7^{b}	2.4 ± 0.9^{ab}	1.8 ± 0.9^{b}	-4.9	***
Water temperature (°C)	6.3 ± 4.8^{a}	6.3 ± 4.3^{a}	9.9 ± 5.9^{a}	9.3 ± 5.7^{a}	19.5	***
Dissolved oxygen (mg/L)	11.5 ± 1.6^{a}	11.7 ± 1.5^{a}	11.1 ± 2.3^{a}	11.1 ± 2.0^{a}	-4.1	***
pH	7.32 ± 0.35^{a}	7.17 ± 0.19^{a}	8.46 ± 0.17^{b}	8.32 ± 0.11^{b}	31.5	***
Specific conductivity (µS/cm)	87 ± 12^{a}	155 ± 8^{b}	1033 ± 278^{c}	1357 ± 441^{d}	61.8	***
TDN (mg/L)	1.2 ± 0.3^{a}	1.4 ± 0.4^{a}	4.9 ± 1.3^{b}	6.5 ± 1.7^{c}	29.2	***
DON (mg/L)	0.06 ± 0.4^{a}	0.3 ± 0.3^{ab}	0.3 ± 0.4^{b}	0.2 ± 0.4^{ab}	-1.5	n.s.
NH_4-N (mg/L)	0.2 ± 0.2^{a}	0.2 ± 0.2^{a}	0.5 ± 0.3^{b}	0.6 ± 0.3^{b}	16.6	***
NO_2-N (mg/L)	0.1 ± 0.2^{a}	<0.01 ± 0^{b}	0.2 ± 0.2^{a}	0.4 ± 0.3^{a}	17.5	***
NO_3-N (mg/L)	0.9 ± 0.3^{a}	0.9 ± 0.2^{a}	3.9 ± 1.1^{b}	5.2 ± 1.6^{c}	36.5	***
TP (mg/L)	0.4 ± 0.3^{a}	0.3 ± 0.3^{ab}	0.2 ± 0.2^{b}	0.3 ± 0.2^{b}	0.5	n.s.
SRP (mg/L)	0.01 ± 0.03^{a}	<0.01 ± 0.00^{a}	0.3 ± 0.2^{b}	0.3 ± 0.2^{b}	31.8	***
DOC (mg/L)	7.9 ± 5.5^{a}	1.9 ± 0.8^{b}	5.5 ± 1.2^{c}	4.1 ± 1.9^{d}	10.5	***
POC (mg/L)	0.8 ± 1.3^{a}	0.9 ± 0.6^{b}	1.3 ± 0.9^{bc}	1.8 ± 0.8^{c}	5.7	***

Table 2. Mean monthly (± SD) inputs of POM (g AFDM m^{-2} mo^{-1}) to the reference and agricultural streams. Differences between land use types were tested with generalized additive models (GAMs) and differences between streams were tested with generalized linear mixed models. Different lowercase letters indicate significant differences between the 4 streams and different uppercase letters indicate a significant difference between reference and agricultural streams.

	Reference			Agricultural		
	Ochsenbach	Wormsgraben	Mean	Sauerbach	Getel	Mean
Total	0.8 ± 1.1^{a}	1.8 ± 1.6^{b}	1.3 ± 1.3^{A}	0.1 ± 0.1^{c}	0.1 ± 0.1^{c}	0.1 ± 0.1^{B}
Leaves	0.5 ± 1^{a}	0.9 ± 1.3^{a}	0.7 ± 1.1^{A}	0 ± 0.02^{b}	0 ± 0.01^{b}	0 ± 0.01^{B}
Wood	0.2 ± 0.3^{a}	0.5 ± 0.6^{b}	0.3 ± 0.4^{A}	0 ± 0^{c}	0 ± 0^{c}	0 ± 0^{B}
Fruit	0.1 ± 0.2^{a}	0.3 ± 0.3^{b}	0.2 ± 0.2^{A}	0 ± 0^{c}	0.01 ± 0.04^{c}	0 ± 0.02^{B}
Herb. veg.	0 ± 0^{a}	0 ± 0.01^{a}	0 ± 0.01^{A}	0.05 ± 0.1^{b}	0.04 ± 0.07^{b}	0.04 ± 0.1^{B}
CPOM	0.04 ± 0.08^{a}	0.07 ± 0.1^{a}	0.06 ± 0.1^{A}	0 ± 0.02^{b}	0 ± 0.01^{b}	0 ± 0.01^{B}

Table 3. Mean monthly (±SD) standing crops of BOM fractions (g AFDM/m^2) in reference and agricultural streams and summaries of GAM model tests for significant differences between land use types and generalized linear mixed model tests for differences between streams. CBOM includes the total of the coarse BOM standing crop (leaves, wood, fruit, herbaceous vegetation, and CPOM). Different lowercase letters indicate significant differences between the 4 streams and different uppercase letters indicate a significant difference between reference and agricultural streams.

	Reference			Agriculture		
	Ochsenbach	Wormsgraben	Mean	Sauerbach	Getel	Mean
Total BOM	484.2 ± 331.4^{a}	205.3 ± 242.1^{b}	344.8 ± 320.9^{A}	348.3 ± 254.9^{ab}	101.4 ± 95.2^{c}	224.9 ± 228.1^{B}
FBOM	147.9 ± 117.1^{a}	21.5 ± 20.9^{a}	81.8 ± 102.7^{A}	184.4 ± 200.3^{ac}	36.5 ± 39.9^{d}	110.0 ± 165.5^{B}
MBOM	74.7 ± 65.8^{a}	20.3 ± 18.2^{b}	44.4 ± 52.1^{A}	35.7 ± 25.6^{c}	15.3 ± 20.7^{bd}	26.2 ± 26.3^{B}
CBOM	261.7 ± 226.2^{a}	163.5 ± 213.2^{b}	212.6 ± 224.1^{A}	128.1 ± 97.1^{bc}	49.7 ± 54.7^{d}	88.9 ± 87.8^{B}
Leaves	30 ± 61.2^{a}	34.7 ± 48.3^{a}	32.3 ± 54.9^{A}	0.4 ± 0.9^{b}	7.2 ± 10^{c}	3.8 ± 7.9^{B}
Wood	145.2 ± 138.9^{a}	85.2 ± 103.2^{a}	115.2 ± 125.3^{A}	27.5 ± 59.8^{b}	7.2 ± 26.3^{c}	17.4 ± 47.1^{B}
Fruit	37.1 ± 78.7^{a}	26 ± 103.6^{a}	31.6 ± 91.7^{A}	1.2 ± 7^{b}	0.3 ± 0.9^{b}	0.8 ± 5^{B}
Herb. veg.	7.1 ± 13.5^{a}	0.4 ± 0.6^{b}	3.8 ± 10.1^{A}	85.6 ± 71.5^{c}	31.6 ± 32.3^{d}	58.6 ± 61.5^{B}
CPOM	42.3 ± 51.5^{a}	17.2 ± 29.3^{b}	29.7 ± 43.5^{A}	13.4 ± 12.9^{b}	3.3 ± 4.8^{c}	8.3 ± 10.9^{B}

Table 4. Summary table displaying results from the 2-sided approach to determine environmental variables associated with OM retention in headwaters of the 2 land-use types. This table shows the relationships between the C spiraling metric V_{OC} and input variables BOC, TOC, and Q; IR with the respective input variables V_{OC} and flow velocity (v); and BOC with the variables discharge (Q) (L/s), hydrological variability (HV), wood BOM (g AFDM/m^2), and POM inputs (g AFDM/m^2). BOC was separated into the compartments FBOM, MBOM, and CBOM and the analysis was done separately for each compartment. All relationships were tested with generalized linear mixed models. OB = Ochsenbach, WG = Wormsgraben, SB = Sauerbach and GE = Getel. Variables connected by an × indicate an interaction. To enhance the clarity of the table, only relationships with significance levels $p < 0.01$ are shown. For a complete description of statistics see Tables S2 and S3.

	Stream	V_{OC} ~	IR ~	BOC ~ hydrological and physical variables		
		BOC, TOC, Q	V_{OC}, v	FBOM	MBOM	CBOM
Reference	OB	BOC	V_{OC}	-	-	Wood
	WG	Q, Q×TOC	V_{OC}, v	Q, Wood	Wood, POM	Wood, POM
Agriculture	SB	BOC, TOC, Q	V_{OC}	HV	HV	-
	GE	BOC, TOC	V_{OC}	Q	Q	-

FIGURE CAPTIONS

Fig. 1. Locations and land use surrounding the 4 study streams in the Harz Mountains, Saxony-Anhalt, Germany.

Fig. 2. Temporal dynamics of POM inputs (g AFDM m^{-2} d^{-1}) from October 2012 to March 2014 in the reference streams Ochsenbach (OB) and Wormsgraben (WG) and in the agricultural streams Sauerbach (SB) and Getel (GE). X-axis labels are months of the year starting with October = 10. Y-axes are on different scales to facilitate comparability between land use types. We sampled twice in April because of the 4-w sampling rhythm, once in the beginning of April and 4 w later at the end of April.

Fig. 3. Mean (± 95% CI) of total BOM, FBOM, MBOM, and CBOM (g AFDM/m^2) in the reference streams Ochsenbach (OB) and Wormsgraben WG) and in the agricultural streams Sauerbach (SB) and Getel (GE) based on monthly values per transect. Different lowercase letters indicate significant differences among the 4 streams as tested by generalized linear mixed models.

Fig. 4. Temporal dynamics of BOM fractions (g AFDM/m^2) in the 2 reference streams Ochsenbach (OB) and Wormsgraben (WG) and the 2 agricultural streams Sauerbach (SB) and Getel (GE). We sampled twice in April because of the 4-w sampling rhythm – once in the beginning of April and 4 w later at the end of April.

Fig. 5. GAM response functions showing the temporal abundance patterns of the log-transformed fractions of FBOM, MBOM, and CBOM in reference and agricultural streams. Dashed lines indicate ~95% CIs around the smooth functions of the interaction sampling date and land use type. The y-axis represents the log-transformed centered response of FBOM, MBOM, and CBOM (g AFDM/m^2). We sampled twice in April because of the 4-w sampling rhythm, once in the beginning of April and 4 w later at the end of April.

Fig. 6. Mean (± 95% CI) velocity of organic C V_{OC} (m/day) and index of retention (IR) in the 2 reference streams Ochsenbach (OB) and Wormsgraben (WG) and the 2 agricultural streams Sauerbach (SB) and Getel (GE). Different lowercase letters indicate significant differences among streams as tested by generalized linear mixed models.

Fig. 7. Mean (± 95% CI) decomposition rates in coarse (k_{total}) and fine mesh (k_{micro}) leaf-litter bags in the 2 reference streams Ochsenbach (OB) and Wormsgraben (WG) and the 2 agricultural streams Sauerbach (SB) and Getel (GE). Different lowercase letters indicate significant differences among streams as tested by generalized linear mixed models.

Fig. 8. Comparison of BOM standing crops found in previous studies and this study in reference and disturbed streams for the fractions of total BOM, CBOM, MBOM, and the ratio between FBOM and CBOM in temperate European and North American headwaters. Abbreviations of streams are as following: OB: Ochsenbach, WG: Wormsgraben (this study); DCC: Devil's Club Creek, CC: Camp Creek, LS: Ledyards Spring, SS: Smith Site Augusta Creek (Minshall et al. 1983); SR: Salmon River Camp Creek (Minshall et al. 1992); HWC: Hugh White Creek, GB: Grady Branch (Golladay et al. 1989); C54, C55 (Lugthart & Wallace 1992), SB: Sauerbach, GE: Getel (this study); LC1: Lapwai Creek Site 1, LC2: Lapwai Creek Site 2 (Delong and Brusven 1993); 2B, 2C, 2E, 2F: Midwestern streams (Griffiths et al. 2012); BHB: Big Hurricane Branch (Golladay et al. 1989). For more detailed information see Table S4.