The influence of floodplain restoration on whole-stream metabolism in an agricultural stream: insights from a 5-year continuous data set

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Abstract: Channelized streams are common in North American agricultural regions, where they minimize water residence time and biological nutrient processing. Floodplain restoration done via the 2-stage-ditch management strategy can improve channel stability and nutrient retention during storms. We examined the influence of floodplain restoration on whole-stream metabolism by measuring gross primary production (GPP) and ecosystem respiration (ER) for 1 y before and 4 y after restoration of an upstream, unaltered control reach and a downstream, restored reach. Both reaches were biologically active and dynamic. GPP ranged from 0.1 to 22.1 g O_2 m^{-2} d^{-1}, and ecosystem respiration (ER) rates ranged from –0.1 to –38.7 g O_2 m^{-2} d^{-1}. We used time-series analysis and found that GPP increased postrestoration during floodplain inundation when expressed per unit length, but not per unit area, of stream. GPP was more resilient post- than prerestoration and returned to prestorm levels more quickly after than before floodplain construction. In contrast, the floodplain restoration had no effect on ER or on any metric of metabolism during base flow. Overall, we showed that floodplain–stream linkages can be important regulators of metabolism in restored agricultural streams.

Key words: whole-stream metabolism, primary production, respiration, two-stage ditch, floodplain, time series analysis

Agriculturally influenced streams are a common feature of the midwestern USA (Blann et al. 2009), where they are managed for maximal drainage, resulting in artificially straightened, trapezoidal channels that lack floodplains (Powell et al. 2006). Agricultural streams receive inputs from an intensively farmed landscape, and as a result, they have open canopies with high light availability, abundant inorganic nutrients, and a predominance of fine-grained sediments (Johnson et al. 1997, Allan 2004, Blann et al. 2009). Therefore, agricultural streams are potential hotspots for biological activity. For example, denitrification rates and nutrient uptake are often elevated relative to less-disturbed streams (Inwood et al. 2005, Mulholland et al. 2008). Despite their predominance in the midwest, agricultural streams are relatively understudied (Martin et al. 2012), even though their characteristics reflect land use across the watershed.

An integrative measure of stream biological activity is metabolism, which is a fundamental ecosystem process that describes the production and consumption of energy in organic matter (Odum and Odum 1955, Fahey and Knapp 2007). Metabolism metrics include gross primary production (GPP; C fixation by autotrophs), ecosystem respiration (ER; C consumption by heterotrophs and autotrophs), and net ecosystem production (NEP; total amount of C accumulated or consumed by an ecosystem). GPP increases with light and nutrient availability (e.g., Young and Huryn 1999, Mulholland et al. 2001, McTammany et al. 2007, Bernot et al. 2010), whereas ER increases with nutrient and organic matter availability, GPP, and temperature (e.g., Hedin 1990, Mulholland et al. 2001, Bernot et al. 2010, Yvon-Durocher et al. 2012). Land use can indirectly influence whole-stream metabolism by altering nutrient availability and riparian shading. In general, agriculturally influenced streams have elevated rates of GPP and ER compared to streams in relatively pristine watersheds (Young and Huryn 1999, McTammany et al. 2003, Bernot et al. 2010). Hydrology can also influence metabolism by deliver-

ing and mobilizing sediments and by disturbing algal populations during storm flows (Morgan et al. 2006, O'Connor et al. 2012). However, we do not know how the presence of floodplains and occurrence of storm flows interact to influence metabolism metrics, particularly in agricultural streams where both flow and floodplain connectivity have been altered.

Floodplains and storm flow are inextricably linked: during storms, water flows onto floodplains, slows down, deposits fine particulate matter, interacts with floodplain soils and vegetation, and increases stream surface area (Gregory et al. 1991, Naiman and Decamps 1997). As a result, the influence of floodplains on metabolism is difficult to disentangle from the influence of elevated stream flow. Agricultural streams typically lack floodplains as a result of repeated dredging to maintain a trapezoidal channel (Fig. 1A). Thus, floodplain restoration offers an opportunity to tease apart the influences of geomorphology and hydrology on ecosystem metabolism in an experimental framework. The 2-stage ditch is an emerging management strategy in which floodplains are constructed beside channelized agricultural streams (Powell et al. 2007b; Fig. 1B). During storms, when nutrient and sediment export is highest and most problematic, stream water flows onto the floodplains, decreasing water velocity, depositing sediments, and improving channel stability (Powell et al. 2007a). In addition, the water flowing onto floodplains interacts with the soil biota and vegetation, which increases reach-scale N removal via deni-

trification (Roley et al. 2012). However, whether concurrent changes occur in whole-stream metabolism is unknown.

Most studies of whole-stream metabolism have been based on periodic or spot measurements. This approach has been useful for identifying controls on GPP and ER, but spot measurements do not allow us to examine the influence of storms and geomorphology. Thus far, continuous data sets have improved estimates of annual net ecosystem production (Uehlinger 2006, Roberts et al. 2007, Izagirre et al. 2008), our understanding of stream response to storms (Uehlinger and Naegeli 1998, Roberts et al. 2007), and identified trends in response to climate change (Marcarelli et al. 2010). However, continuous metabolism data have yet to be used in an experimental context. Furthermore, only 2 studies have incorporated temporal autocorrelation into the analysis of continuous metabolism data, despite the high potential for autocorrelation in continuous data (Marcarelli et al. 2010, Solomon et al. 2013).

In a typical 2-stage ditch, the restored floodplains are at least as wide as the baseflow channel, a feature that triples the stream width during inundation (Powell et al. 2007b; Fig. 1B). The floodplains are inundated frequently (Powell et al. 2006), and at our study site, water flowed onto the floodplains an average of 12 times/y (Roley et al. 2012; Table 1). Given these inundation patterns, restored floodplains may influence stream metabolism via 2 pathways: 1) turbidity reduction, and 2) increased bioreactive surface area for assimilatory activity. Two-stage floodplains potentially reduce streamwater turbidity during storms (U. H. Mahl, JLT, RTD, and SSR, unpublished data), which could increase light penetration to the benthos and subsequently increase GPP rates. In addition, the increase in stream surface area during floodplain inundation may increase reach-scale ER and GPP.

We used 5 y of continuous metabolism data collected within an experimental framework to evaluate how floodplain restoration influences whole-stream metabolism. The 5-y data set allowed us to examine annual and seasonal patterns in metabolism and to assess the trophic state of a high-light, high-nutrient, agriculturally influenced stream. We hypothesized that floodplain restoration would increase GPP and ER during storm flow, but not during base flow. Specifically, we expected that floodplain inundation during storms would reduce turbidity and increase GPP, and that the increase in bioreactive surface area from floodplain creation would increase GPP and ER. We did not expect metabolism metrics to change at base flow because floodplain restoration in and of itself does not influence the geomorphology of the stream channel during baseflow conditions. Floodplain restoration could have made the stream channel less shaded by moving the steep ditch banks further from the stream. However, the grassy vegetation immediately adjacent to the stream was not removed or damaged, and even though the ditch banks were further from
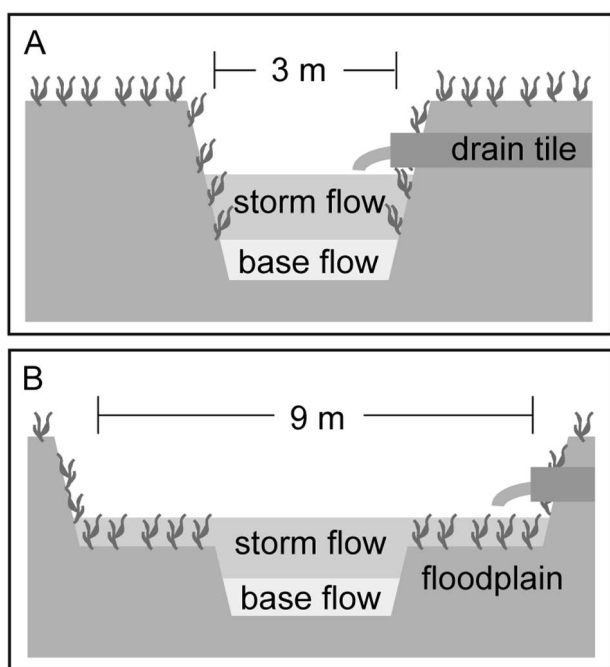

Figure 1. A.—A conventional agricultural ditch. B.—A 2-stage ditch, with floodplains added. Note that the baseflow channel dimensions did not change.

Table 1. Frequency and duration of floodplain inundation by year.

Year	Events	Minimum duration (d)	Median duration (d)	Mean duration (d)	Maximum duration (d)
2008	11	1	8	12.3	53
2009	16	1	3.5	7.9	60
2010	10	2	7.5	10.3	22
2011	11	2	6	12.6	35

the stream, their steep angle did not change. Thus, we expected that any decrease in shading would be minimal. The restoration could also decrease delivery of organic matter to the stream channel by allowing fine particles to settle on the floodplains instead of in the stream channel (Powell et al. 2007b). However, the study stream already had large accumulations of fine benthic organic matter, so we did not expect that a decreasing supply of fine particles would influence metabolism over the time frame of our study. We tested the above hypotheses with an extensive data set consisting of continuously measured whole-stream metabolism, which allowed us to examine metabolism across all seasons and to differentiate between baseflow and stormflow responses.

METHODS
Study site and experimental design

Shatto Ditch is in north-central Indiana, in the Tippecanoe River watershed. More than 80% of the Shatto Ditch subwatershed is in row-crop agriculture, primarily a maize–soybean rotation, and it receives inputs from subsurface tile drains (Fig. 1A, B). As a result, Shatto Ditch has consistently high dissolved inorganic nutrient concentrations. During our 5-y study, the mean concentration of NO_3^- was 5.3 mg N/L, NH_4^+ was 65 μg N/L, and soluble reactive P was 43 μg P/L. In addition, Shatto Ditch has a flashy hydrograph, with most high-flow events occurring in winter and spring. Discharge ranged from 12 to ~2000 L/s and median discharge (Q) was 63 L/s. Over the 5 y, Shatto averaged 12 bankfull events/y (defined as flows that inundated floodplains, $Q > 109$ L/s, Table 1, Figs 1B, 2A; Roley et al. 2012). Bankfull events varied in duration from <1 d to 60 d (Table 1). In general, the floodplains were inundated more frequently in spring, although inundation events occurred throughout the year.

To examine the effect of floodplain restoration on whole-stream metabolism, we used a before/after–control/impact (BACI) study design (Stewart-Oaten et al. 1986). We established two 600-m reaches along Shatto Ditch: an upstream control reach (CTL) and a downstream treatment reach (TRT) where floodplains were constructed. Both reaches had similar surrounding land use and nutrient concentrations, but the upstream CTL reach had lower Q and slightly more riparian woody shrubs than the

TRT reach. We accounted for these differences with the BACI design. We collected metabolism data for nearly 1 y (January–November 2007) in both reaches prior to floodplain restoration, and then constructed the floodplains on the TRT reach and continued to collect metabolism data for 4 more years (November 2007–December 2011) in both reaches. During restoration, the stream channel itself was not altered and the grasses immediately adjacent to the stream were left intact. Stream turbidity did not increase during the restoration, and we observed very little erosion of the newly excavated floodplain. After construction, the floodplains were seeded with grasses and forbs, and the floodplains were fully vegetated after 1 growing season. The vegetation on the floodplains did not appear to cause any more shading than grasses slumping into the stream from the banks of the trapezoidal channel (SSR, personal observation).

Metabolism calculations

We placed Hydrolab MS 5 data sondes (Hach, Loveland, Colorado) at the downstream end of the TRT and CTL reaches and programmed them to record dissolved O_2 (DO), temperature, and turbidity every 30 to 60 min. Every 2 wk, we downloaded and field-calibrated the sondes and replaced the batteries. We deployed the sondes inside perforated polyvinyl chloride (PVC) pipes for protection from stream debris and animals, and attached the pipes, oriented parallel to stream flow, to fence posts pounded into the stream bottom. We also deployed photosynthetically active radiation (PAR) sensors and water-level capacitance meters to record data at 30- to 60-min intervals (Odyssey, Christchurch, New Zealand).

We used our field data to estimate GPP and ER with the 1-station, open-channel method in the upstream CTL reach (Odum 1956) and the 2-station open-channel method in the TRT reach (Odum 1956, Marzolf et al. 1994, Young and Huryn 1998). We used the 2 approaches because of equipment availability and to be sure that our estimates reflected solely the reach of interest. Specifically, in the TRT reach, we estimated the upstream distance integrated with the 1-station method as $3V/K$, where V is stream velocity (m/d) and K is reaeration rate (/d) (Chapra and DiToro 1991), and found that it would encompass the entirety of both reaches. Therefore, to constrain the metabolism esti-
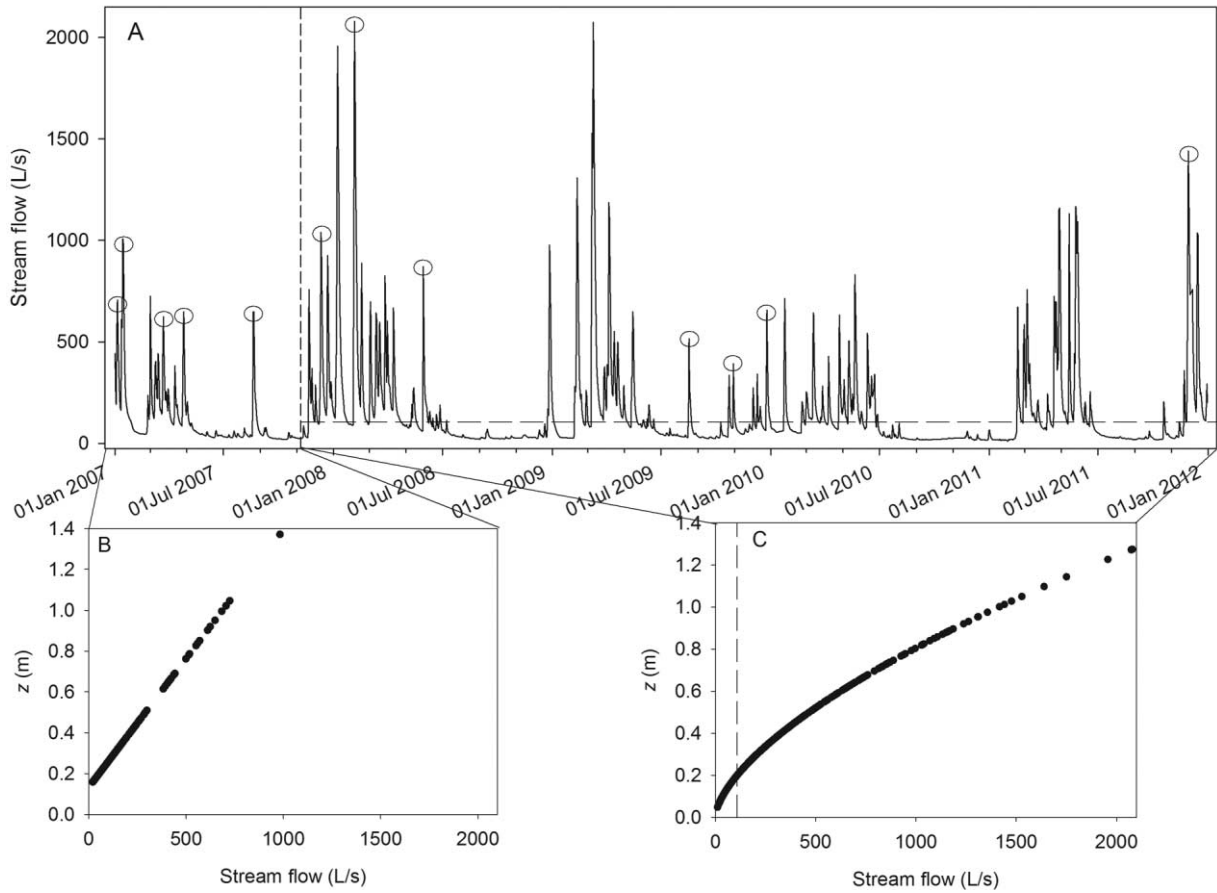
Figure 2. Discharge (Q) in the treatment (TRT) reach (A) and the regression relationship between Q and depth (z) before (B) and after (C) restoration. In panel A, the vertical dashed line represents the 2-stage ditch restoration date and circles indicate the storms analyzed for resistance and resilience. The horizontal line in panel A and the vertical line in panel C represent the Q at which water begins to flow onto the floodplains.

mates to the TRT reach only and to accurately examine the effect of the floodplain restoration, we used the 2-station approach. We could not do the same for the CTL reach because of a lack of sondes, but the CTL reach is a homogenous channelized stream all the way to its headwaters, so small day-to-day variation in the upstream distance integrated had minimal influence on GPP and ER. To validate our approach further, we compared the 1-station and 2-station models for the TRT reach in the prerestoration year. GPP estimates were ~25% lower with the 2-station method, whereas ER estimates were equivalent when –5 g O_2 m^{-2} d^{-1} > ER > –15 g O_2 m^{-2} d^{-1}. When ER was >–5 g O_2 m^{-2} d^{-1}, the 2-station model was ~20% higher, but when ER <–15 g O_2 m^{-2} d^{-1}, the 2-station model was ~20% lower. These small differences may reflect the different reach lengths integrated by the 2 methods or some inherent bias. Nevertheless, with the BACI statistical approach, we were comparing the difference between the TRT and CTL reaches pre- and postrestoration, not the absolute difference between the reaches, and so it is most

important for us to ensure that our method delineates the appropriate reach.

The equation for 1-station metabolism is:

$$\frac{dC}{dt} = (\text{GPP} - \text{ER} + K\text{D}) \qquad \text{(Eq. 1)}$$

where D is the O_2 surplus or deficit (Odum 1956). In the daytime regression method, we replaced this equation with:

$$\frac{\Delta[O_2]_i}{\Delta t} = AI_t^\rho - \text{ER}(1.072^{(temp_i - temp_{ave})}) + K(1.024^{(temp_i - temp_{ave})})D_t \qquad \text{(Eq. 2)}$$

where A is the light use efficiency factor (the proportion of light used for photosynthesis), I_t is solar irradiance at time (t), and ρ is an exponent that allows for light saturation when $\rho < 1$ (Kosinski 1984, Atkinson et al. 2008). Both ER (in g O_2 L^{-1} d^{-1}) and K are corrected for temperature at each time step. We used a temperature-

dependence factor of 1.072 for ER (Atkinson et al. 2008), and 1.024 for K (Kilpatrick et al. 1989). The values of A, ρ, ER, and K are iteratively solved by minimizing the sums-of-squares between the measured and modeled DO concentration (Atkinson et al. 2008, Griffiths et al. 2013), with a Marquardt algorithm in ModelMaker 4.0 (AP Benson, Wallingford, UK). For each 24-h period over the 5-y data set, we ran the model 6 times, each time with different starting values, and used the results with the best goodness-of-fit coefficient (r^2). Parameter starting values had little effect on the goodness-of-fit or parameter estimates, which usually fell within 10% of one another for all model runs.

In the TRT reach, we used the 2-station method, in which metabolism is calculated based on the difference in DO between the upstream (CTL) station and the downstream (TRT) station. The basic 2-station equation is:

$$O_2 down_{t0+\tau} = O_2 up_{t0} + (\text{GPP} + \text{ER} + K\text{D})\tau \quad \text{(Eq. 3)}$$

where $O_2 down_{(t0+\tau)}$ is downstream DO (mg/L) following travel time τ (d), and $O_2 up_{(t0)}$ is the upstream DO concentration at time 0 (Odum 1956, Marzolf et al. 1994, Young and Huryn 1998). We calculated travel time for each date, based on relationships between Q and V (see below) and the known distance between sondes. We assumed that GPP was a linear function of light, took the average DO deficit for the upstream and downstream stations and made substitutions to arrive at the following equation:

$$O_2 down_{t0+\tau} = \left[O_2 up_{(t0)} + \frac{\text{GPP}}{z} \times \frac{\sum_{t0}^{t0+\tau}\text{PAR}}{\Sigma\text{PAR}} + \frac{\text{ER}}{z}\tau \right. $$
$$\left. + K\tau \frac{Osatup_{(t0)} - O_2 up_{(t0)} + Osatdown_{(t0+\tau)}}{2} \right]$$
$$/ \left[1 + \frac{K\tau}{2} \right]$$
$$\text{(Eq. 4)}$$

where ΣPAR is the total daily PAR, $\sum_{t0}^{t0+\tau} PAR$ is the PAR accumulated during the travel time τ, $Osatdown_{(t0+\tau)}$ is downstream DO saturation, $Osatup_{(t0)}$ is the upstream DO saturation, and z is mean stream depth. We solved for ER, GPP, and K over a 32-h period by minimizing the negative log-likelihood of the model relative to the data, using function nlm in R (ROH, unpublished method). Infrequently, the model returned unreasonable numbers, such as positive values for ER or negative values for GPP, and these values often were associated with estimates of K that were inexplicably high or low. For all dates where ER > 0 or < –40 g O_2 m^{-2} d^{-1}, GPP < 0 g O_2 m^{-2} d^{-1}, K < 0, or K > 40/d, we re-ran the model with K fixed at the seasonal average for that year, which often resulted in an improved fit and realistic results. If rerunning with a fixed K resulted in a poorer model fit or continued to return

unreasonable results, we removed that date from our data set. Variation in K, which ranged from 1/d to 39/d was considerable, but was low compared to higher-gradient streams. For example, Mulholland et al. (2001) reported K from 20 to 300/d in 1st- to 3rd-order streams across North America. Time-series analysis revealed that variation in K was mostly explained by K on the previous day and by changes in Q (data not shown). Overall, Shatto Ditch was well suited to our modeling approach because the stream is biologically active and low gradient. Variation in K had a small effect on GPP. Last, for each date, we calculated NEP as GPP + ER.

The 1-station model includes a term for light saturation (light increases linearly until saturation is reached), whereas the 2-station model assumes a linear relationship with light. We saw no evidence of light saturation in the 1-station model, and GPP increased linearly with light (data not shown). Therefore, the lack of a light saturation term did not bias our 2-station results. In addition, we tested the effect of the light saturation term by running a subset of data through 2 different 1-station models, 1 with and 1 without a light saturation term, and compared the results on individual days. The 2 models returned results that were highly correlated (r^2 = 0.98 for GPP and r^2 = 0.93 for ER), with a slope near 1 and an intercept near 0 (GPP = 1.33x – 0.12; ER = 1.27x – 0.32, where GPP or ER was estimated from the model with the light saturation term, and x was GPP or ER estimated without the light saturation term). In other words, the model with the light saturation term returned slightly higher values (~30% higher), but these small differences are unlikely to influence our interpretation, especially given that we used a BACI design (as described above). Furthermore, differences between the reaches appeared to be independent of the method used. If the differences were driven by the different methods, we would expect to see consistently higher values of both GPP and ER in the CTL reach. Instead, we found that CTL ER values were 45% lower than TRT ER values, on average, and CTL GPP values were lower than the TRT reach during autumn and winter and higher during spring and summer. Thus, the observed differences between reaches appear to be driven largely by underlying physical conditions, rather than by methodological differences.

We were unable to correct for groundwater inputs when making metabolism calculations because flow accumulation in the watershed is largely from tile drains, rather than from ground water. Ground water is typically low in DO, which means that the magnitude of our GPP and ER estimates may have been underestimated (Hall and Tank 2005). However, our GPP and ER estimates span a very large range and approach some of the highest reported rates in the literature (see Results), even without the ground-water correction. This finding suggests that Shatto Ditch has an overriding biological signal, in spite of any ground-

water contributions. Furthermore, because we compared an upstream CTL and downstream TRT reach and because 2-stage ditch construction probably did not affect groundwater recharge (i.e., no change in postconstruction TRT discharge relative to the CTL), our conclusions regarding the influence of floodplain restoration are not affected by the lack of groundwater correction.

Estimates of assimilatory uptake

Quantifying the potential influence of floodplain restoration on metabolism has intrinsic value, but metabolism metrics are not always readily translated to management applications. We related metabolism directly to the 2-stage ditch as a management tool by using our metabolism data to estimate assimilatory N uptake, which we assumed to be a temporary N removal mechanism (Mulholland et al. 2000). Then we compared the assimilation estimates to stream denitrification, which permanently removes N from the system (Galloway et al. 2003). To estimate rates of assimilatory N removal, we calculated the fraction of GPP respired by autotrophs by estimating the slope of the 90th quantile on a regression between GPP and ER (Hall and Beaulieu 2013). We multiplied that number by GPP and then subtracted it from GPP to get the amount of primary production available for uptake by heterotrophs. We converted the units from g O_2 m^{-2} d^{-1} to g C m^{-2} d^{-1}, assuming a photosynthetic quotient of 1.2 (Bott 2006), and then converted to g N m^{-2} d^{-1}, using a previously published mean C:N ratio of 12 for algae (Dodds and Priscu 1990, Webster et al. 2003), thus arriving at autotrophic assimilatory N uptake. To estimate the heterotrophic portion of assimilatory N uptake, we calculated heterotrophic respiration by subtracting the amount of GPP that was respired from ER. We converted the units from g O_2 m^{-2} d^{-1} to g C m^{-2} d^{-1}, assuming a respiratory quotient of 0.85 (Bott 2006) and then multiplied by 0.22, which is an estimate of mean bacterial growth efficiency (del Giorgio and Cole 1998). In this calculation, we assumed that most of the heterotrophic uptake is bacterial and fungal, which is reasonable for this agricultural stream with very low invertebrate diversity and a low abundance of fish. Last, we converted the units to g N m^{-2} d^{-1}, using a mean C:N ratio for heterotrophic bacteria of 5 (Fenchel et al. 1998). We added autotrophic and heterotrophic assimilation together to estimate total N assimilation. This stoichiometric approach does not double-count assimilatory N uptake because microorganisms probably will preferentially take up water-column N over particulate N because of high dissolved nutrient concentrations in these streams (Webster et al. 2003, Hamilton et al. 2004).

Depth and Q calculations

We used a water-yield relationship with the nearby Eel River US Geological Survey (USGS) gauge (North Man-

chester, Indiana, USGS 03328000) to estimate daily Q over the 5-y study at Shatto Ditch with the following equation:

$$Q_{\text{Shatto}} = \frac{Q_{\text{Eel}} \times L_{\text{Shatto}}}{L_{\text{Eel}}} \qquad \text{(Eq. 5)}$$

where Q is discharge and L is the land area drained, with subscripts denoting the stream name. Midway through the study period, we deployed capacitance meters (Odyssey, Christchurch, New Zealand) at Shatto Ditch and found a 1-d delay between the capacitance meter hydrograph and the Eel River hydrograph, so we adjusted our calculations of Q accordingly.

To calculate average stream depth, we created a Q to z relationship in each reach (Gore 2006). We used the slug-release method to measure velocity in the CTL reach and prerestoration TRT reach. On each release date, we measured width (w) every 20 m along the reach, and then calculated depth as $z = Q/(Vw)$. In addition, we confirmed that our calculated Q (from the water-yield relationship) was similar to our measured Q (using salt slugs). In the postrestoration TRT reach, we created a discharge–depth relationship from manual depth measurements at evenly spaced transects (every 20 m) on numerous dates encompassing both baseflow and storm-flow conditions because we were unable to find a statistically significant relationship between discharge and slug-calculated depth as a result of changes in channel morphology. At each transect, we measured depth every 10 cm, and averaged all depth measurements for the reach.

We framed our storm data within the context of the flow regime at Shatto by using flow-duration curves to calculate the probability of exceedance (P), which is the probability that Q on any given day will be higher than Q on the storm date. To calculate P, we first ranked Q on each day from largest to smallest. Next, we calculated P as:

$$P = \frac{1}{(n+1)/m} \times 100 \qquad \text{(Eq. 6)}$$

where m is the Q rank and n is the number of days in the data set (Gore 2006).

Statistical analysis

Our data set encompassed 5 y of daily metabolism data and showed strong temporal autocorrelation, so we used an auto-regressive integrated moving average (ARIMA) model (Box and Jenkins 1970) to account for the autocorrelation. We estimated 3 sets of parameters, including the auto-regressive (AR) parameters (p), which include coefficients that link the response variable at time t with the response variable at previous time periods. We also esti-

mated moving average (MA) coefficients (q), which link the error term of previous time steps with the response variable at time t. If the data were not stationary, i.e., if they did not have a constant mean, variance, and autocorrelation, we first detrended the data by differencing (Cryer and Chan 2008). If the data required 1 order of differencing, then they had a trend with a constant rate of change. If the data required 2 orders of differencing, then they had a trend with a nonconstant rate of change.

The structure of an ARIMA model is denoted by (p, d, q), where p = the number of auto-regressive parameters, d = the order of differencing, and q = the number of moving average parameters. To assess if we had properly accounted for autocorrelation, we plotted the autocorrelation function and the partial autocorrelation function, which plot the residuals at a series of time lags and indicate the presence or absence of autocorrelation (Zuur et al. 2009). For all models that adequately accounted for autocorrelation, we chose the best model by comparing Akaike's Information Criterion (AIC; Akaike 1973). We also included a seasonal component (i.e., a SARIMA model), but SARIMA models had higher AIC values and poorer fits than those models without the seasonal component.

We used the response variables ΔGPP and Δ|ER|, where ΔGPP is the difference between TRT GPP and CTL GPP for each day, and Δ|ER| is the difference between the absolute value of TRT ER and the absolute value of CTL ER for each day. In doing so, we always examined metabolism metrics for the TRT relative to the CTL. In addition to the autocorrelation parameters, we used Q, stream temperature, total daily PAR, and streamwater turbidity as potential explanatory variables. We also used GPP as an explanatory variable for Δ|ER|. We completed the ARIMA analysis on the prerestoration data and postrestoration data separately. If the 2-stage ditch influenced metabolism metrics, we would expect to see a difference in the structure or in the coefficients between prerestoration and postrestoration models. We also completed the ARIMA analysis on GPP and ER in each individual reach (i.e., CTL and TRT) to assess the drivers of metabolism.

We examined storms separately from baseflow conditions because we had predicted that we would see the greatest changes in GPP and ER during storms as a result of floodplain inundation. We defined storms as dates when $Q > 109$ L/s in the TRT reach, which corresponded to stream water just beginning to flow onto the floodplains. For this comparison, we expressed ΔGPP and Δ|ER| 2 ways: 1) areally (as g O_2 m^{-2} d^{-1}), as in the time-series analysis, and 2) linearly (as g O_2 m^{-1} d^{-1}), to assess the effect of increased stream width. To calculate linear ΔGPP and Δ|ER|, we multiplied the areal rate by stream width (m) on that day. Because storms are discrete, independent events, we did not account for temporal autocorrelation

and instead used stepwise linear regression to compare prerestoration and postrestoration ΔGPP and Δ|ER| on storm dates. To avoid autocorrelation within a single storm, our replicates were an average ΔGPP and Δ|ER| for each storm, instead of multiple individual dates within a single storm. To avoid correlation among potential explanatory variables, we tested variables for collinearity and eliminated those that were correlated (i.e., we eliminated temperature because it was correlated with light). Explanatory variables included the maximum or average Q during the storm, average light during the storm (as an indicator for season), and a dummy variable that coded for prerestoration (0) or postrestoration (1). For Δ|ER|, we also included ΔGPP as an explanatory variable. If the dummy variable was significant, then restoration influenced storm ΔGPP or Δ|ER|. If the intercept was significant, then ΔGPP or Δ|ER| had a non-0 mean (i.e., it was higher in one reach than the other). If the other explanatory variables were included in the best-fit model, then the difference between the reaches was influenced by season (light) or by storm intensity (Q). We used the same approach to compare total N removal pre- and postrestoration.

We also calculated resilience and resistance of metabolism metrics to storms (following Uehlinger 2006). We represented storm resilience as the number of days required for GPP or ER to return to prestorm levels, with a longer recovery time to predisturbance rates indicating lower resilience. Resistance was the relative change in GPP or ER, in response to a storm. We calculated resistance as:

$$R = 1 - \frac{X_{before} - X_{after}}{X_{before}} \qquad \text{(Eq. 7)}$$

where X is either GPP or ER (Uehlinger 2006). For both GPP and ER, the prestorm value was the average value for the 2 to 5 d prior to the peak storm Q, and the poststorm value was the average value for 2 to 5 d immediately after the storm. The variation in days was a result of data availability. We aimed for 5 d pre- and 5 d poststorm but were sometimes restricted to fewer days because of data availability. We compared the effect of floodplain restoration on resilience and resistance metrics with a t-test on the difference between reaches. We also analyzed the effect of storm size on resistance and resilience metrics by regressing resistance and resilience in each reach with peak Q and with P. We restricted resistance and resilience analysis to storms for which we had ≥2 d of data immediately before and immediately after the storm in both reaches.

We completed all statistical analyses in R. For the time-series analysis, we used the *arima* function in the TSA library. The *arima* function allows for missing data in the time-series analysis (i.e., it is not necessary to have measurements on every day), so we did not fill data gaps. For the stepwise linear regression, we used the *step* function.

RESULTS
Geomorphology and Q

After the restoration, the addition of floodplains resulted in a substantial difference in stream geomorphology, which was reflected in the relationship between Q and z in the TRT reach. Prior to the restoration, the relationship between Q and z was linear (Fig. 2B), but after the restoration, Q and z had a power relationship, with a lower z for each Q (Fig. 2C). The changes in geomorphology had potential consequences for metabolism during storm flow. During storms, the TRT reach was wider and shallower with increased surface area for GPP and ER.

Metabolism metrics

The 2-station and 1-station models were able to estimate metabolism on >75% of the dates for which we had DO, temperature, and light data (TRT = 960/1259 d, CTL = 1075/1345 d). The days that were not modeled successfully had either a very small diel change in DO, which usually occurred in the winter, or an atypical DO curve (e.g., DO decreased throughout the day), which usually occurred during storms.

Shatto Ditch was a biologically active and dynamic stream, with GPP ranging from 0.1 to 22.1 g O_2 m^{-2} d^{-1} in the CTL and 0.1 to 12.1 g O_2 m^{-2} d^{-1} in the TRT reaches (Fig. 3A). We also examined the data by season, with the seasons defined by day length (e.g., spring occurs from the vernal equinox through the summer solstice). GPP had a strong seasonal signal, with the highest rates occurring in spring (CTL: 4.5 ± 3.2 [SD] g O_2 m^{-2} d^{-1}, TRT: 3.4 ± 2.1 g O_2 m^{-2} d^{-1}) and the lowest rates occurring in the winter (CTL: 0.8 ± 1.2 g O_2 m^{-2} d^{-1}, TRT: 0.8 ± 0.7 g O_2 m^{-2} d^{-1}). In both reaches, ER had a wider range of values (CTL: –0.1 to –38.7 g O_2 m^{-2} d^{-1}, TRT: –0.1 to –38.4 g O_2 m^{-2} d^{-1}; Fig. 3B). As with GPP, ER was highest in spring (CTL: –6.1 ± 4.0 g O_2 m^{-2} d^{-1}, TRT: –12.0 ± 6.6 g O_2 m^{-2} d^{-1}), but lowest in autumn (CTL: –3.3 ± 2.6 g O_2 m^{-2} d^{-1}, TRT: –3.8 ± 3.2 g O_2 m^{-2} d^{-1}). The CTL reach exhibited more variability in GPP than did the TRT reach (coefficient of variation [CV] for CTL GPP = 1.2, CV for TRT GPP = 0.9). The 2 reaches had the same CVs for ER (CTL and TRT CV = 0.8) and had similar ranges of ER.

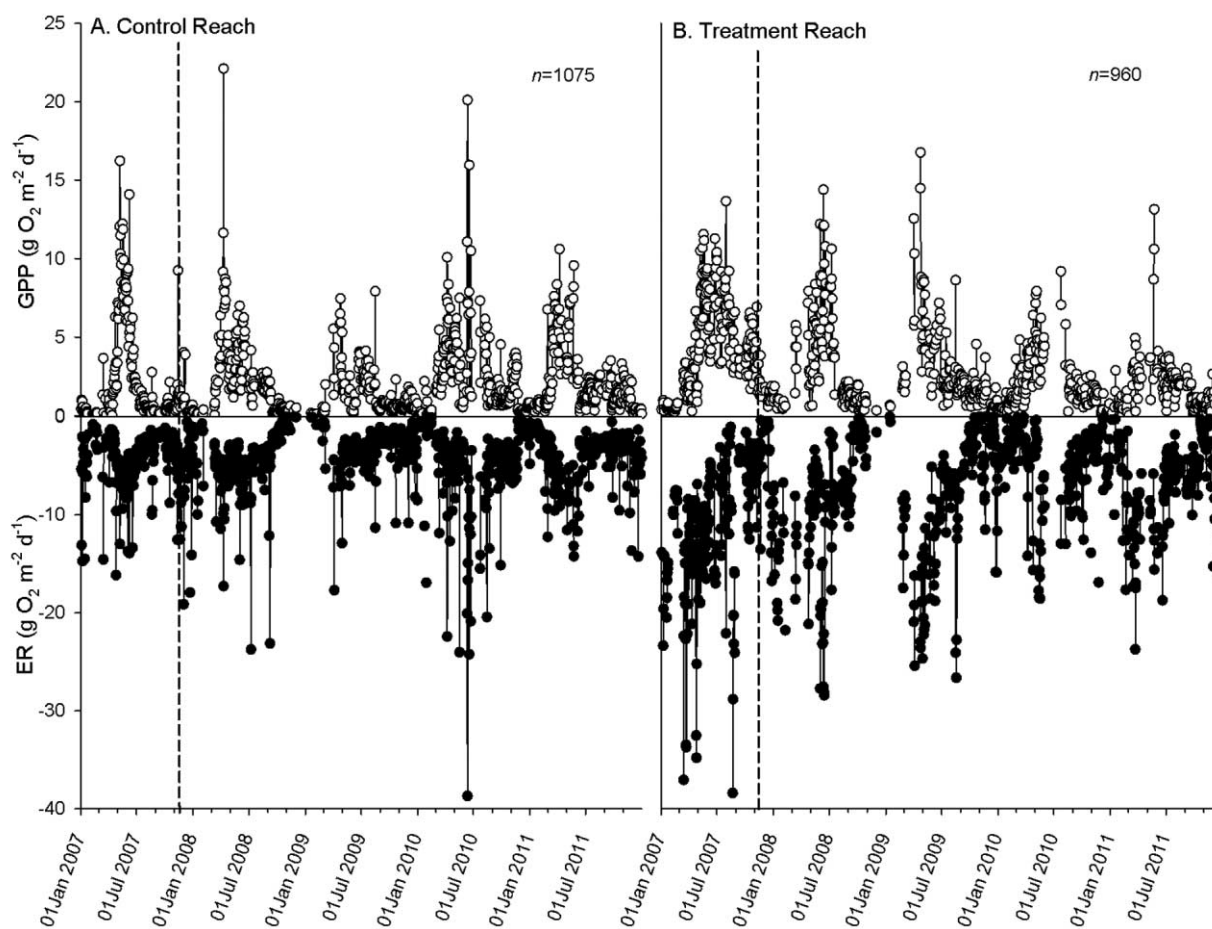After accounting for autocorrelation, the best predictor of GPP in the CTL reach was Q. GPP increased

Figure 3. Gross primary production (GPP) and ecosystem respiration (ER) in the control (CTL) (A) and treatment (TRT) (B) reaches. Vertical dashed lines represent the 2-stage ditch restoration date.

slightly with Q (Table 2). In contrast, the best predictors of GPP in the TRT reach were light and temperature. GPP increased with both variables. The difference in best-fit models probably was a result of contrasting channel characteristics. The CTL reach was more shaded, smaller, and more constrained than the TRT reach. However, the coefficients on all predictors were small (e.g., a doubling in Q increased CTL GPP by only 50%; Table 2) suggesting that Q, temperature, and light each had a minor effect on GPP. The best predictor of ER in both the TRT and CTL reaches was GPP (Table 2), showing that GPP and ER were tightly coupled. In addition, GPP from the previous 2 d was also a significant predictor of ER, suggesting that GPP had a lagged and sustained influence on ER (data not shown).

Shatto Ditch was heterotrophic (NEP < 0) most of the time (Fig. 4A), which is consistent with observations in other streams (Battin et al. 2008, Marcarelli et al. 2011; Fig. 4B). The CTL reach was autotrophic for only 10% of all measurements (87 of 870 d), whereas the TRT reach was autotrophic for only 7% of all measurements (64 of 870 d). In the CTL reach, most of the autotrophic days occurred in spring, when autotrophy occurred 34% of the time (78 of 229 d). In contrast, the CTL reach was autotrophic for only

2% of autumn (5 of 249 d), 3% of winter (4 of 140 d), and never in summer (0 of 252 d). In the TRT reach, autotrophic days were spread out more evenly among seasons, with autotrophy occurring during 12% of autumn (31 of 249 d), 5% of spring and summer (12 of 229 and 13 of 252 d, respectively), and 6% of winter (8 of 140 d).

Effects of floodplain restoration on metabolism

To estimate how floodplain restoration altered metabolism, we fit an ARIMA model to pre- and postrestoration data, using ΔGPP and Δ|ER| as our response variables. The postrestoration best-fit models for ΔGPP and Δ|ER| had the same structure as the prerestoration model, and the coefficients were not statistically different from one another (Table 2). Thus, floodplain restoration did not influence the overall pattern of metabolism in Shatto Ditch. All models had a 1st-order of differencing, which suggests that ΔGPP and Δ|ER| had a constant trend, but that trend was not consistently increasing or decreasing (Fig. 5A, B).

The best pre- and postrestoration model for ΔGPP was a (0, 1, 1) ARIMA model without additional predictor variables (Table 2, Fig. 5A). The prerestoration model was $\Delta GPP_t = \Delta GPP_{t-1} - 0.62\varepsilon$, whereas the postrestoration model was $\Delta GPP_t = \Delta GPP_{t-1} - 0.65\varepsilon$, where ε is the differ-

Table 2. Structure of the auto-regressive integrated moving average (ARIMA) model for the difference between the treatment (TRT) and control (CTL) reaches in gross primary production (ΔGPP) and ecosystem respiration (Δ|ER|) pre- and postrestoration. The model structure is (p, d, q) as described in Methods. SE = standard error, TGPP = GPP in the TRT reach, CGPP = GPP in the CTL reach, PAR = mean daily photosynthetically active radiation, Temp = mean daily water temperature, Q = mean daily discharge, θ is the moving average coefficient, φ is the auto-regressive coefficient, $\beta 0$ is the intercept, $\beta 1$ = the coefficient on the 1st explanatory variable, $\beta 2$ = the coefficient of the 2nd explanatory variable.

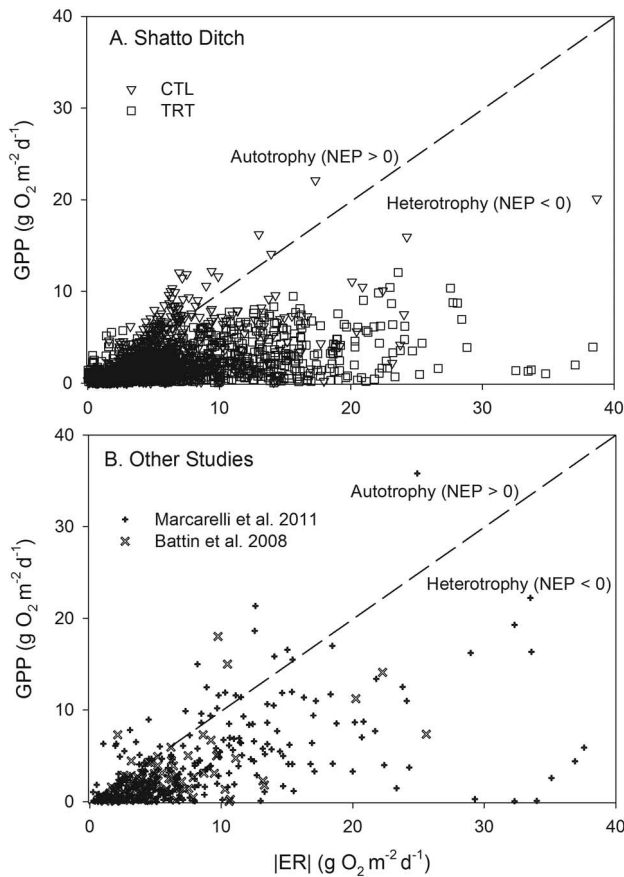| Response	ARIMA model structure	Component	Prerestoration coefficient	SE	Postrestoration coefficient	SE	Coefficient (all data periods)	SE
ΔGPP	(0, 1, 1)	θ	−0.62	0.05	−0.65	0.03		
Δ|ER|	(1, 1, 1) + TGPP	φ	0.37	0.19	0.33	0.09		
		θ	−0.76	0.12	−0.82	0.05		
		β	1.60	0.24	1.20	0.13		
GPP – CTL reach	(1, 1, 1) + Q	φ					0.09	0.07
		θ					−0.64	0.05
		β					0.002	0.001
GPP – TRT reach	(1, 1, 1) + PAR + Temp	φ					0.34	0.06
		θ					−0.82	0.03
		$\beta 1$					0.04	0.01
		$\beta 2$					0.2	0.03
ER – CTL reach	(1, 0, 1) + CGPP	φ					0.89	0.02
		θ					−0.56	0.05
		$\beta 0$					2.0	0.25
		$\beta 1$					1.12	0.07
ER – TRT reach	(1, 1, 1) + TGPP	φ					0.76	0.03
		θ					−0.96	0.01
		$\beta 1$					1.70	0.09

Figure 4. Daily autotrophy and heterotrophy in the 2 study reaches (A) and in 2 meta-analyses of metabolism measurements (B). Points that fall above the 1 : 1 line indicate autotrophy (net accumulation of organic matter on that day) and points that fall below the 1 : 1 line indicate heterotrophy (net consumption or export of organic matter on that day). CTL = control reach, TRT = treatment reach, NEP = net ecosystem production.

Figure 5. Difference in gross primary production (ΔGPP) (A) and in ecosystem respiration (Δ|ER|) (B) between the treatment (TRT) and control (CTL) reaches with the results of the best-fit auto-regressive integrated moving average (ARIMA) model. Points that fall above 0 are the dates on which the TRT reach had higher rates, and points that fall below 0 are the dates on which the CTL reach had higher rates. The dashed line represents the restoration date. See Table 2 for regression abbreviations.

ence between the model and the actual data on the previous day. These models indicate that the best predictor for ΔGPP was solely the ΔGPP from the previous day.

The best pre- and post-restoration model for Δ|ER| was a (1, 1, 1) ARIMA model with GPP in the TRT reach as an additional predictor variable (Table 2, Fig. 5B). The prerestoration model was $\Delta|ER|_t = 1.37\Delta|ER|_{t-1} - 0.76\varepsilon + 1.6TGPP$, whereas the best postrestoration model was $\Delta|ER|_t = 1.33\Delta|ER|_{t-1} - 0.83\varepsilon + 1.2TGPP$, where TGPP is GPP in the treatment reach. These models suggest that divergence in ER between the reaches probably is a result of autotrophic respiration (AR), and that TRT ER increases with TRT GPP. Total daily PAR was a statistically significant predictor of both Δ|ER| and ΔGPP, but its presence did not improve model fits, so we eliminated it from the model. All of the variation that could be explained by light availability was explained by ΔGPP or
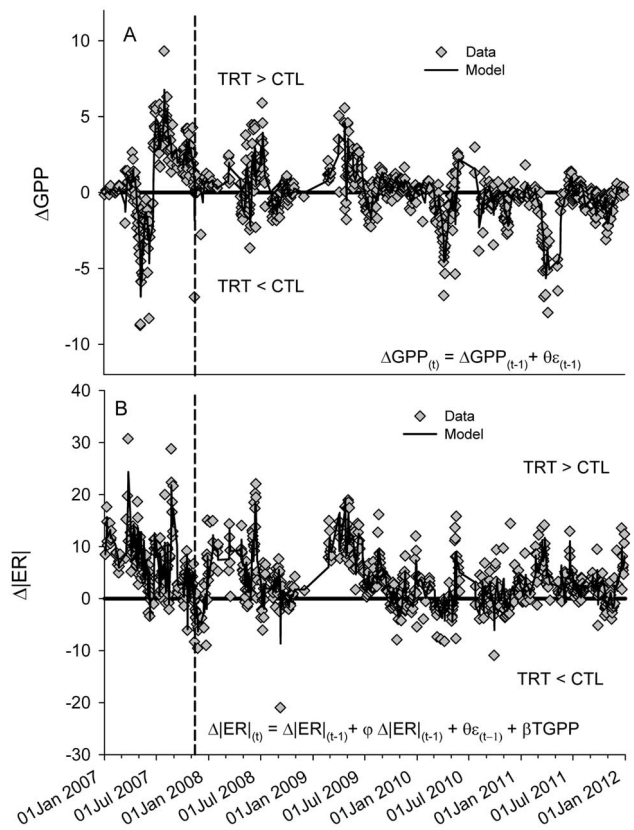
Δ|ER| from the previous day. All other predictor variables, including Q, temperature, and turbidity, were not statistically significant predictors of the difference in metabolism between the TRT and CTL reaches.

Effect of floodplain inundation on metabolism

The ARIMA models provided robust fits for our 5-y data set, but they were unable to capture all of the variation in ΔGPP and Δ|ER|, which was particularly evident for the highest and lowest values (Fig. 5A, B). We examined all dates that were not captured by the model, and found that 73% of the Δ|ER| and 38% of the ΔGPP values not captured by the model occurred during floodplain inundation, which is when we expected to see a floodplain effect on metabolism. To estimate the extent to which floodplain restoration influenced metabolism during storm flow, we examined the storm data, which included 208 measurement dates, encompassing 46 storms over the 5 y. We

found no statistically significant predictor variables for ΔGPP, expressed in g O_2 m^{-2} d^{-1} (p = 0.166; Fig. 6A), which suggests that storm GPP did not change postrestoration, nor was it consistently different between reaches. In other words, the floodplain restoration did not change area-specific rates of GPP because of, e.g., more algae or more macrophytes per unit area. However, when we examined ΔGPP in a linear fashion, expressed as g O_2 m^{-1} d^{-1} (i.e., primary production per length of stream), we found that it was higher postrestoration and that it increased with Q and with light (stepwise regression, r^2 = 0.26, $p < 0.01$; Fig. 6B, Table 3). On average, storm-flow ΔGPP was 2 g O_2 m^{-1} d^{-1} prerestoration and increased to 6 g O_2 m^{-1} d^{-1} postrestoration, a 3× increase (Fig. 6B). The increase in ΔGPP with Q probably was caused by the increased stream surface area during storms.

In contrast, stepwise regression revealed that areal $\Delta|$ER$|$ (expressed /m^2) decreased postrestoration. On average, it was 2.3× lower (Fig. 6C, Table 3). The other explanatory variables were light and ΔGPP, which suggests that ER was tightly coupled to GPP. $\Delta|$ER$|$ expressed linearly (g O_2 m^{-1} d^{-1}) did not change postrestoration

(Fig. 6D, Table 3), and the only explanatory variable was ΔGPP. Thus, even though areal rates of ER during storms declined in the TRT reach relative to the CTL reach, we found no change in linear ER, probably because the increase in surface area from floodplains made up for the decrease in areal rates of ER.

Floodplain restoration increased the resilience of GPP. The average time to recovery poststorm was 2.4 d shorter postrestoration (t-test of differences, p = 0.021). In contrast, floodplain restoration had no effect on the resilience of ER or the resistance of GPP or ER (t-test of differences, $p > 0.2$ for all tests; Table 4). In general, storms had a stronger effect on GPP than on ER. Specifically, the mean resilience of ER ranged from 1.8 ± 2 to 4.0 ± 3 d. In contrast, the mean resilience of GPP ranged from 3.8 ± 3 to 16.9 ± 11 d (Table 4). After some winter storms, GPP did not return to the prestorm rates until the following spring. Storms frequently stimulated ER. More than 80% of storms had higher ER after than before the storm, whereas <40% of storms had higher GPP after than before storms (Table 4). Neither storm peak Q nor P was related to resistance or resilience (SLR, $p > 0.2$ for all).
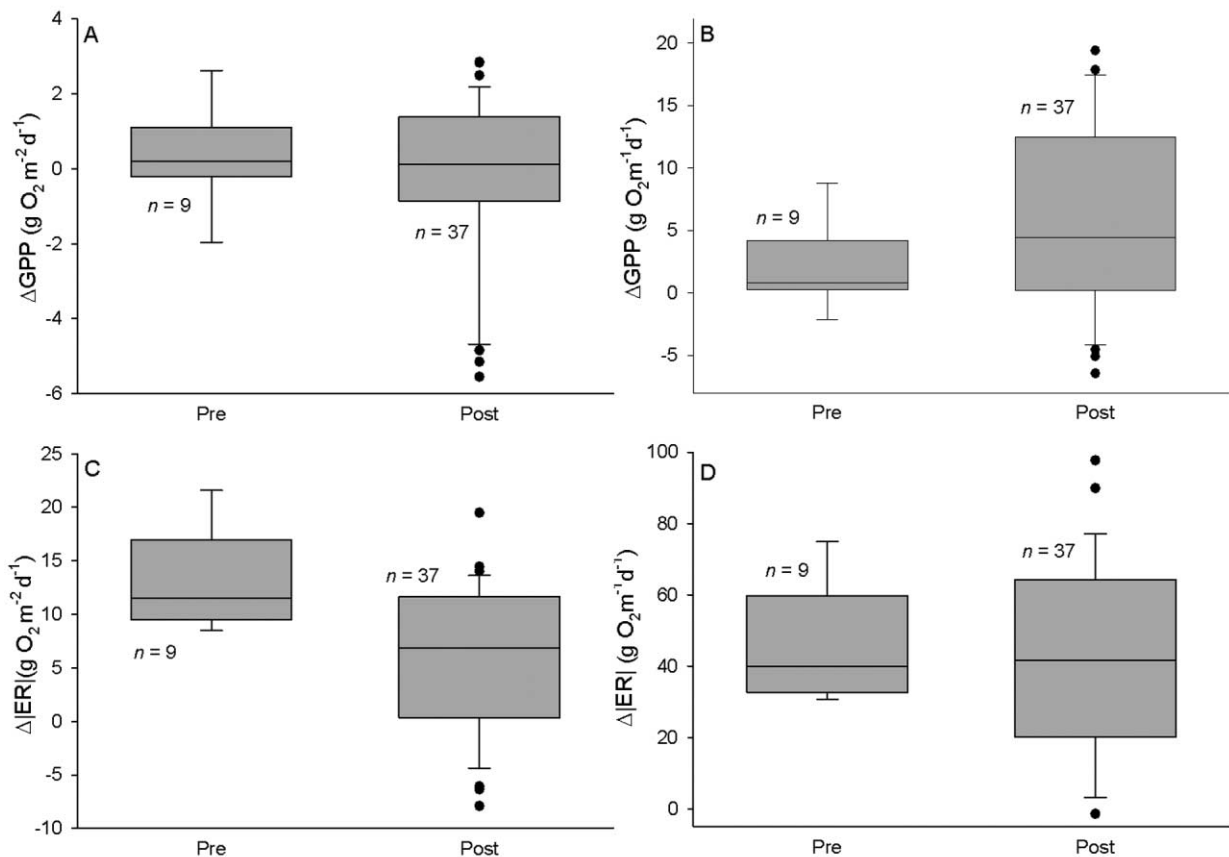

Figure 6. Difference between treatment and control reach in gross primary production (ΔGPP) (A, B) and ecosystem respiration ($\Delta|$ER$|$) (C, D) during storm flow, expressed areally (g O_2 m^{-2} d^{-1}) (A, C) and per length of reach (g O_2 m^{-1} d^{-1}) (B, D) pre-restoration (Pre) and postrestoration (Post). Lines in boxes show medians, box ends show quartiles, whiskers show 90th and 10th percentiles, and circles show outliers.

Table 3. Parameters for best-fit stepwise regressions of storm metabolism data. We did not find a statistically significant model to describe storm ΔGPP (areal). The result here is the best-fit model, but it was not statistically significant. Restoration = prerestoration or postrestoration. A positive number indicates higher values postrestoration, Q_max = the highest discharge (Q) during the storm, PAR = mean photosynthetically active radiation during the storm.

Y	X	Coefficient	Model r^2	Model p
Δ total N removal (areal) (g N m^{-2} d^{-1})	Intercept	0.14	0.23	0.001
	Restoration	−0.11		
	PAR	0.01		
Δ total N removal (linear) (g N m^{-1} d^{-1})	Intercept	0.22	0.17	0.007
	Q_max	0.01		
	PAR	0.03		
ΔGPP (areal) (g O$_2$ m^{-2} d^{-1})	Intercept	−0.7	0.02	0.17
	Q_max	0.002		
ΔGPP (linear) (g O$_2$ m^{-1} d^{-1})	Intercept	−8.7	0.26	0.001
	Restoration	4.5		
	Q_max	0.01		
	PAR	0.43		
Δ|ER| (areal) (g O$_2$ m^{-2} d^{-1})	Intercept	9.2	0.26	0.001
	ΔGPP	0.79		
	Restoration	−7		
	PAR	0.24		
Δ|ER| (linear) (g O$_2$ m^{-1} d^{-1})	Intercept	34.9	0.17	0.002
	ΔGPP	1.56		

Assimilatory uptake of N

We estimated that 60% of GPP was respired immediately by autotrophs in both the TRT and CTL reaches (quantile regression). GPP and heterotrophic respiration (HR = ER – AR), were highly correlated (Pearson's correlation, $r = 0.883$ in CTL reach, $r = 0.993$ in TRT reach), suggesting that GPP was tightly coupled to both autotro-

phic and heterotrophic respiration. We used our AR estimates to calculate assimilatory N uptake and found that autotrophic N removal in the TRT reach ranged from 0 to 0.18 g N m^{-2} d^{-1} and averaged 0.06 ± 0.04 g N m^{-2} d^{-1}, whereas autotrophic N removal in the CTL reach ranged from 0 to 0.19 g N m^{-2} d^{-1} and averaged 0.03 ± 0.04 g N m^{-2} d^{-1}. Heterotrophic N removal was

Table 4. Resistance and resilience of gross primary production (GPP) and ecosystem respiration (ER) to storms by reach (CTL = control reach, TRT = treatment reach) and date (pre = prerestoration, post = postrestoration). Resistance is the relative change in GPP or ER (mean ±1 SD). It was unchanged postrestoration for both GPP and ER. Resilience is the mean (±1 SD) number of days to return to prestorm values, with a lower value indicating greater resilience. GPP resilience increased postrestoration in the TRT relative to the CTL, but ER resilience was unchanged. Storm stimulation is the number of times storms stimulated metabolism (GPP or ER increased after the storm).

Reach	Time	Metric	Resistance	Resilience (d)	Storm stimulation (occurrences/total no. storms)
CTL	Pre	GPP	2.1 ± 0.5	3.8 ± 3	2/5
TRT	Pre	GPP	1.1 ± 1.0	5.2 ± 3.9	3/5
CTL	Pre	ER	2.1 ± 0.7	2.8 ± 3.3	4/5
TRT	Pre	ER	2.5 ± 0.5	1.8 ± 2.0	5/5
CTL	Post	GPP	0.5 ± 0.4	16.9 ± 10.9	1/7
TRT	Post	GPP	1.1 ± 0.9	7.6 ± 9.0	3/7
CTL	Post	ER	1.8 ± 1.2	1.4 ± 1.2	5/7
TRT	Post	ER	2.2 ± 1.4	4.0 ± 3.2	6/7

generally higher than autotrophic N removal. In the TRT reach, heterotrophic N removal ranged from 0 to 0.60 g N m^{-2} d^{-1} and averaged 0.16 ± 0.10 g N m^{-2} d^{-1}, whereas heterotrophic N removal in the CTL reach ranged from 0 to 0.23 g N m^{-2} d^{-1} and averaged 0.04 ± 0.03 g N m^{-2} d^{-1}. Total N removal (heterotrophic + autotrophic) in the TRT reach ranged from 0.05 to 0.68 g N m^{-2} d^{-1} and averaged 0.22 ± 0.10 g N m^{-2} d^{-1}, whereas total N removal in the CTL reach ranged from 0.01 to 0.27 g N m^{-2} d^{-1} and averaged 0.07 ± 0.05 g N m^{-2} d^{-1}. Overall, assimilatory N uptake varied seasonally and mirrored GPP, with more variation and higher rates of heterotrophic uptake in the TRT than CTL reach.

Autotrophic N removal and heterotrophic N removal were converted directly from GPP and ER, respectively, so the N removal statistics showed the same patterns as ΔGPP and Δ|ER|. Autotrophic N removal increased during postrestoration storms when expressed linearly (/m of stream reach), but did not change when expressed areally (/m^2 of stream reach). As with ER, heterotrophic N removal was lower postrestoration when expressed areally and unchanged when expressed linearly. Stepwise regression of total N removal (autotrophic + heterotrophic) revealed that areal total N removal (g N m^{-2} d^{-1}) was higher prerestoration (Table 3). The best model for linear total N removal (g N m^{-1} d^{-1}) revealed no change in total N removal postrestoration (Table 3). Thus, even though linear GPP increased during storms, N uptake remained unchanged, probably because ER was typically higher than GPP and because heterotrophs have a lower assumed C:N ratio and, thus, take up more N per unit biomass than autotrophs.

DISCUSSION
Drivers explaining variation in metabolism metrics

Using time-series analysis, we found that ΔGPP and Δ|ER| were highly autocorrelated, a result suggesting that daily variation in light and temperature influenced the 2 reaches similarly. We also found that GPP in the TRT reach was a positive, significant predictor of Δ|ER|. Thus, as TRT GPP increased, so did the difference in ER between the reaches. Most likely, this effect was caused by higher AR, which contributed to ER, in the TRT than the CTL reach. When reaches were examined separately, we found strong autocorrelation and that ER increased with GPP. The relationship between GPP and ER suggests that AR was a substantial component of ER. Indeed, the quantile regression method estimated that 60% of GPP was respired immediately, and GPP and HR were highly correlated, suggesting tight coupling between autotrophs and heterotrophs.

Studies in which whole-stream metabolism was compared across multiple streams have identified numerous predictor variables, including nutrient concentration, temperature, V, light, and sediment organic matter content (e.g., Mulholland et al. 2001, Bernot et al. 2010). After accounting for autocorrelation, we found that GPP increased most strongly with temperature in the TRT reach and with Q in the CTL reach, although the coefficients on both temperature and Q were small (i.e., for each 1°C increase in temperature, GPP increased by 0.2 g O$_2$ m^{-2} d^{-1}). The best predictor of ER in both reaches was GPP, which further emphasizes the high level of AR in Shatto Ditch. Marcarelli et al. (2010) similarly found that the best time series model for continuous metabolism included temperature and GPP or ER from the previous day. Therefore, after accounting for autocorrelation, GPP and ER in this agricultural stream are influenced by previously identified drivers of metabolism.

The influence of floodplains on metabolism

The model structure and coefficients were consistent through time for both ΔGPP and Δ|ER|, showing that floodplain restoration did not change how metabolism metrics responded to environmental conditions (e.g., light availability, temperature). This finding was not surprising because most measurements occurred during baseflow conditions (Figs 2A, 3A, B), when we did not expect a floodplain effect. Instead, we had predicted that floodplains would increase storm-flow GPP, expressed linearly (g O$_2$ m^{-1} d^{-1}) and areally (g O$_2$ m^{-2} d^{-1}), but we found an increase in linear GPP only. Contrary to our predictions, turbidity was not a significant predictor of GPP or ΔGPP (Table 2). Therefore, any postrestoration turbidity reduction did not lead to a concurrent increase in areal GPP. We did observe a 3× increase in linear storm GPP (g O$_2$ m^{-1} d^{-1}) as a result of increased stream surface area during floodplain inundation. Floodplain restoration created a wider storm-flow channel, which increased the capacity for ecosystem processes (Sweeney et al. 2004).

In contrast, areal Δ|ER| (g O$_2$ m^{-2} d^{-1}) decreased postrestoration during storms, a result suggesting that floodplain respiration was lower than stream-channel respiration. Lower floodplain respiration may be a result of lower organic matter content on floodplain soils. Organic matter content was more spatially variable on floodplains than in the stream channel and included patches of low and high quantity and quality (Roley et al. 2012). In addition, we may have underestimated ER during the rising and falling limbs of a storm, when vegetation was not fully submerged. Emergent leaves of anaerobic-tolerant grasses, including the common species at our site (reed canary grass, *Phalaris arundinacea*, and rice cut grass, *Leersia oryzoides*) can provide some O$_2$ to the rhizosphere when soils are saturated (Miller and Zedler 2003, Pierce et al. 2009), thereby stimulating ER without a corresponding drawdown in stream-water O$_2$. However, the surface water is not likely to be exchanged with water in the rooting zone, so we do not think

oxidation of the rhizosphere fully explains the postrestoration change in ER. Last, lower ER could be caused by lower AR rates of floodplain grasses than of stream algae, but vascular plants typically have higher AR than algae (e.g., Cole et al. 1992, Duarte and Cebrian 1996, DeLucia et al. 2007). Moreover, the increase in surface area during storms resulted in no change in linear ER, which suggests that floodplain restoration did not change ER over the entire restored reach.

The presence of floodplains increased the resilience of GPP, but had no effect on the resilience or resistance of ER to storms. We note that the increased resilience was relative to the CTL reach. Mean resilience decreased in both reaches postrestoration, but the decrease was lower in the TRT reach (Table 4). The decrease in mean resilience was a result of 2 postrestoration winter storms that yielded long recovery times. In general, storms depress GPP more than ER, and ER is often stimulated by storm flows (Uehlinger 2006, Roberts et al. 2007). Our results were consistent with these previous observations and suggest that floodplains can significantly mitigate the influence of storms on GPP, thereby potentially altering stream response to disturbance. One important consequence of increased GPP resilience may be maintenance of assimilatory nutrient uptake during storms, which is when agricultural streams typically export the most nutrients (Royer et al. 2006). Overall, we found that altering channel geomorphology, via floodplain restoration, altered the stream metabolic response to changing hydrology (i.e., storms).

Continuous metabolism data confirm the predominance of heterotrophy

These high-light, high-nutrient agricultural streams were dynamic, biologically active ecosystems, yet they were heterotrophic for most of the year. In general, flowing waters are heterotrophic and consume more C than they produce (Rosenfeld and Mackay 1987, Cole and Caraco 2001, Mulholland et al. 2001, Battin et al. 2008). To place our data in context of previously studied streams, we compared our data to 2 meta-analyses of metabolism measurements made in temperate, semi-arid, and tropical streams and rivers (Battin et al. 2008, Marcarelli et al. 2011). Similar to streams included in the meta-analyses, Shatto Ditch was rarely autotrophic (NEP > 1), despite being an open-canopy stream with high inorganic nutrient concentrations (Fig. 4A). Streams receive allochthonous subsidies because of their location on the landscape and their tight linkage with their catchment, so even highly productive streams with high light availability tend to be heterotrophic (Rosenfeld and Mackay 1987, Frankforter et al. 2010, Marcarelli et al. 2011). We would expect frequently autotrophic streams, if they exist, to have open canopies (high light availability) and high nutrient availability. Shatto Ditch meets both of these criteria, but it was heterotrophic

for most of the year (Fig. 4A) because it is tightly connected to terrestrial habitats and receives large inputs of terrestrial OM, resulting in fine-grained, organic-matter-rich benthic sediments (Roley et al. 2012), which generally support high rates of ER (Hedin 1990, Bernot et al. 2010, Griffiths et al. 2013). Thus, an additional requirement for consistent autotrophy would be geomorphic characteristics that result in dominance of inorganic substrata (e.g., cobble, gravel) or that prevent accumulation or inputs of terrestrial organic matter in the stream (i.e., steep slope, routinely scouring flows). Uehlinger (2006) reported regular autotrophy in a high-nutrient, open-canopy, gravel-bed stream.

N removal and floodplain management

In a previous study, we measured denitrification every 2 mo in Shatto Ditch to assess the effect of floodplain restoration on removal of NO_3-N (Roley et al. 2012). We used those denitrification data and the N-assimilation estimates from this study to estimate the fraction of total N uptake associated with assimilatory N uptake. We divided total assimilatory uptake by total inorganic N uptake, defined as denitrification plus assimilatory uptake, on dates on which we measured denitrification. On average, assimilatory uptake accounted for 37% of total N uptake in the CTL reach and 47% of total uptake in the TRT reach with floodplains. This calculation demonstrates that assimilatory N uptake is a potentially substantial contributor to N removal rates in Shatto, although its contribution is not as high as measured in previous studies. In comparison, in a study of NO_3^- uptake in 72 streams of varying land use, the median NO_3^- uptake from assimilatory uptake was 84%, with a range from 0 to 99.5% (Mulholland et al. 2008). The large range reported by Mulholland et al. (2008) was nearly captured in our single stream because of seasonal changes. In the CTL reach, the assimilatory uptake fraction ranged from 4% in winter (December 2008) to 82% in early summer (June 2008), and in the TRT reach, it ranged from 16% in winter (November 2009) to 86% in spring (April 2009). Therefore, during spring and early summer, the assimilatory uptake fraction in Shatto Ditch approached the median value reported by Mulholland et al. (2008), but at other times of the year, denitrification played the more dominant role in N uptake. Autotrophs are seasonally light-limited (Roberts et al. 2007), but denitrifiers typically are limited by NO_3^- and organic C availability (Inwood et al. 2005, Mulholland et al. 2008), which are abundant throughout the year in Shatto Ditch (Roley et al. 2012). Continuous metabolism data used to estimate assimilatory N uptake is a powerful tool for gaining insight on temporal patterns. Our analysis highlights the potential for seasonal changes in the dominant ecosystem processes in a single stream.

Our method for estimating assimilatory uptake is based on the assumption that most N uptake comes from the

water column. If heterotrophs were getting some N from organic matter, then we would have overestimated assimilatory uptake to some degree. However, we would have overestimated assimilatory uptake in the same way on both reaches, so we think that our main conclusions remain valid: 1) assimilatory uptake shows large seasonal fluctuations, and 2) floodplain restoration had no effect on assimilatory uptake rates.

Overall, floodplain restoration can increase inorganic N uptake from agricultural streams by increasing surface area for assimilatory uptake and denitrification during floods. The benefits of floodplain restoration are most apparent during inundation, so floodplains should be constructed at a low elevation that floods frequently. Seeding or planting of perennial vegetation on restored floodplains may further increase N removal via vegetative assimilatory uptake.

Conclusions

Geomorphology and hydrology interacted to influence whole-stream metabolism, and restoration of floodplains in formerly channelized streams can alter metabolism metrics during storms. During base flow, floodplains did not influence whole-stream metabolism, but during storms, floodplains effectively widened the stream, which increased GPP. Floodplains increased the resilience of GPP to storms and buffered the potential effects of disturbance. Overall, we showed that restored floodplains can regulate whole-stream metabolism during floodplain inundation. Stream management strategies should consider floodplain–stream connections and the role of hydrology in linking these adjacent habitats to optimize restoration efforts.

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