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Ecosystem metabolism in coastal plain streams of southeast Louisiana : environmental and watershed effects

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ECOSYSTEM METABOLISM IN COASTAL PLAIN STREAMS OF SOUTHEAST
LOUISIANA: ENVIRONMENTAL AND WATERSHED EFFECTS

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The Department of Renewable Natural Resources

by

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This dissertation is dedicated to the memory of Michael O. West (1965 – 2010)

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TABLE OF CONTENTS

ACKNOWLEDGMENTS	iii
ABSTRACT.....	vi
CHAPTER 1. CONTRIBUTIONS OF OPEN-SYSTEM METHODS TO STREAM METABOLISM THEORY: A MINI-REVIEW	1
Introduction.....	1
Factors Controlling GPP and ER	3
Methodology.....	8
Scope.....	10
References.....	11
CHAPTER 2. SEASONAL VARIATION IN STREAM METABOLISM IN SHADED AND UNSHADED SAND-BOTTOM STREAMS OF THE SOUTHEASTERN LOUISIANA COASTAL PLAIN.....	17
Introduction.....	17
Methods and Materials.....	19
Results.....	23
Discussion.....	32
References.....	41
CHAPTER 3. MULTIVARIATE ANALYSES OF ECOSYSTEM METABOLISM IN COASTAL PLAIN STREAMS IN SOUTHEAST LOUISIANA: EFFECTS OF STREAM SIZE AND LAND USE PATTERNS	47
Introduction.....	47
Methods and Materials.....	50
Results.....	56
Discussion.....	68
References.....	76
CHAPTER 4. EXTREME EVENTS AFFECT ECOSYSTEM METABOLISM IN A SANDY, COASTAL PLAIN STREAM OF LOUISIANA	83
Introduction.....	83
Methods and Materials.....	85
Results.....	90
Discussion.....	99
References.....	106
CHAPTER 5. CONCLUSIONS	110
Synopsis of Previous Chapters.....	110
Future Directions and Conclusions.....	111
References.....	114

APPENDIX. SOURCE TABLES FOR VARIOUS ANOVAS USED IN THIS DISSERATION	117
VITA.....	119

ABSTRACT

Since its introduction in 1956, the use of open-system, diel dissolved oxygen curves for estimating the components of ecosystem metabolism in the lotic setting have been important in determining the current ecosystem theory of streams, both spatially among multiple systems and longitudinally within the same system, as well as identifying potentially impaired systems, especially when contrasted with streams considered unimpaired. Several factors have been identified as controls on both components of ecosystem metabolism and include light, nutrients, and stable substrates for gross primary production (GPP) and a source of organic matter (OM) for ecosystem respiration (ER). Stream size is important at mediating these factors through the presence or absence of a riparian canopy where small streams tend to have an intact canopy that can severely limit light to primary producers but provide a good source of OM for respiration. Alternatively, larger systems tend to lose canopy cover via widening of the stream and the limitation of light is relaxed while input of OM decreases. Additionally, inputs from watershed land use can affect GPP and ER in the stream via the inputs of nutrients to stimulate algal growth or organic pollution that stimulates heterotrophic activity. In the following studies, the effect of the presence or absence of a riparian canopy, watershed land use, and stochastic events such as flooding on ecosystem metabolism in coastal plain streams of southeast Louisiana are described. These systems behave similarly to previous studies and provide more evidence that the use of ecosystem metabolism as a metric for stream health is beneficial. Recommendations for future studies include the identification of more unimpaired systems while adding a temporal component, modeling systems under different hydrologic or climate change regimes, and the assessment of the impacts of stochastic events such as extreme weather events, exotic species invasions, or local extirpations of important species.

CHAPTER 1. CONTRIBUTIONS OF OPEN-SYSTEM METHODS TO STREAM METABOLISM THEORY: A MINI-REVIEW

Introduction

Howard T. Odum originally introduced the use of diurnal oxygen curves as a technique to estimate open-system stream metabolism in his seminal work at Silver Springs, Florida (Odum, 1956, 1957). Essentially treating the entire ecosystem as an organism that both produces and respire oxygen, he showed that important ecosystem metabolic processes can be estimated for any stretch of flowing water through the algebraic sum of primary production, respiration, and diffusion (reaeration) into and out of the water. As no autotrophic production is occurring at night, ecosystem respiration (ER) is determined by subtracting diffusion rates from the nocturnal rate of change in dissolved oxygen concentration, and by extrapolating these rates through daylight hours, gross primary production (GPP) can be calculated (Odum, 1956). In the decades since Odum's work, many methodological improvements and alterations have streamlined the measurement and accuracy of GPP and ER (Marzolf et al., 1994, 1998; Young and Huryn, 1998; Hall and Tank, 2005; Roberts et al., 2007). Importantly, these improvements have led to the potential application of ecosystem metabolism as an integrative functional metric of stream health (Fellows et al., 2006; Young et al., 2008). Due to the development of low-cost *in situ* instrumentation, it can be easily added to any existing or forthcoming monitoring program, and can be used to calculate GPP and ER from previously recorded diel oxygen curves (Izagirre et al., 2008).

The components of ecosystem metabolism provide information as to whether the energy from organic matter (OM) that fuels the lotic food web originates from allochthonous or autochthonous sources. One way to assess the trophic nature of the system is to compare the

ratio of GPP to ER, or P/R (Bott, 2006). If most of the OM comes from upstream sources, the riparian canopy, or the floodplain, the stream is considered net heterotrophic and the P/R ratio is less than 1. In contrast, if production by algae and/or other aquatic plants is supporting the food web, P/R ratios usually exceed 1 and the system is considered to be net autotrophic. Whether the stream functions as a net heterotrophic or net autotrophic system can vary both spatially and temporally and can be strongly influenced by environmental factors such as temperature, solar radiation, and turbidity (Odum, 1956). Another metric used to assess a stream's trophic status is net ecosystem production (NEP), also called net daily metabolism (NDM; Bott, 2006). Calculated as $GPP - ER$, its interpretation is similar to P/R, i.e., positive and negative values of NEP are indicative of autotrophy and heterotrophy, respectively. Although P/R and NEP rates can be used interchangeably, many studies will focus on either one metric or the other in discussing trophic status.

In addition to open-system methods, there are several other techniques for estimating the components of ecosystem metabolism, including benthic chambers, C^{14} uptake (Bott, 2006), or organic matter budgets (e.g., Fisher et al., 1982; Minshall et al., 1983). However, over the past two decades, more and more open-system studies are being completed, which likely reflects the simplicity of data collection and importance of ecosystem metabolism rates to stream research (Tank et al., 2010). Consequently, the purpose of this mini-review is to summarize the factors that control GPP and ER based on results from open-system methods. I will include a few studies based on other methodologies due to their importance in establishing general ecosystem metabolism theory or as models predicting both spatial and temporal patterns in GPP and ER. I am not minimizing the importance of other methods in establishing or advancing the theory of stream metabolism, and in fact, many of these methods have been seminal in establishing current

stream theories and paradigms (see reviews by Young et al., 2008; Tank et al., 2010).

Additionally, this mini-review will serve as the introduction to the remainder of my dissertation.

Factors Controlling GPP and ER

The river continuum concept (RCC) proposed by Vannote et al. (1980) predicted patterns of metabolism along a continuum from headwater streams to large rivers and provided a canvas for testable hypotheses in subsequent metabolism studies. The RCC predicts that the presence of a riparian canopy that shades headwater (1st – 3rd order) streams restricts light penetration and limits autotrophic production, but also provides an abundant supply of allochthonous OM input. As the stream widens (4th – 6th order), the canopy opens up and allows greater light availability to the stream benthos, promoting increased production by autotrophs and an autochthonous OM-based trophic web. In larger rivers (>6th order), water becomes deep and turbid, minimizing autotrophic production, with system productivity becoming more dependent on OM from upstream or floodplain sources. As a consequence of these changes in the importance of heterotrophy or autotrophy, P/R ratios also change along this continuum, initially low in shaded small streams, increasing in mid-reach streams as primary production increases, and decreasing again in larger, more turbid rivers.

Stream research based on open-system metabolism measurements has supported many of the predictions of the RCC where an important factor controlling stream productivity is sunlight, usually estimated from measurements of stream width, canopy cover, or photosynthetically active radiation (PAR). For example, smaller streams tend to have lower production rates, and GPP and P/R ratios tend to increase with increasing stream order or width along a river continuum (McTammany et al., 2003; Ortiz-Zayas et al., 2005) or among streams at regional or

inter-biome scales (Mulholland et al., 2001; Bott et al., 2006; McTammany et al. 2007; Bernot et al, 2010). However, geography plays an important role in this relationship, as headwater streams in grassland, prairie, and desert systems usually lack a gallery forest and an overstory canopy, and are usually considered net autotrophic (Minshall, 1978; Fisher et al., 1982; Dodds et al., 1996; Mulholland et al., 2001). Interestingly, in grassland or prairie streams, a gallery forest develops at higher stream orders and net heterotrophic conditions can occur, inverting the pattern predicted by the RCC (Wiley et al., 1990). The RCC goes on to predict that as streams increase in size, depth or turbidity reduce light penetration and autotrophic production, which is consistent with patterns of GPP reported by Young and Huryn (1996) for the lower reaches of the Taieri River in New Zealand. Other factors influencing light availability to the stream include the sun's orientation, high valley walls, and channel entrenchment (Young and Huryn, 1999; Acuña et al., 2004; Young et al., 2008). Light limitation of GPP also varies temporally due to: (1) seasons, with spring leaf growth in the canopy significantly decreasing light availability to the stream or leaf litter floating on the stream surface in fall (Hill et al., 2001; Acuña et al., 2004; Roberts et al., 2007; Izagirre et al., 2008); (2) annual fluctuations in rainfall, with increased storm frequency resulting in greater turbidity and depth (Young and Huryn, 1996; Izagirre et al., 2008) and benthic scouring (Uehlinger and Naegeli, 1998; Uehlinger, 2000; 2006); (3) stochastic variations in daily cloud cover (Young et al., 2008); and (4) longer-term changes associated with the loss or expansion of the riparian canopy, often related to deforestation (McTammany, et al., 2007; Riley and Dodds, 2012).

In addition to light, several other factors have been implicated as potential controls on stream GPP. Although nutrients are usually not considered limiting to ecosystem processes in lotic systems (Larned, 2010), some species of nitrogen and phosphorus have been shown to be

important correlates of GPP. For example, increased ambient concentrations of soluble reactive phosphate (SRP) were associated with higher GPP in several studies across large spatial scales in North America (Lamberti and Steinman, 1997; Mulholland et al., 2001). Similarly, higher rates of GPP were found in streams categorized as eutrophic due to chronic nutrient enrichment in Spain (Izagirre et al., 2008), and both excess phosphate and nitrate were associated with high GPP rates in agriculturally-developed watersheds (Wiley et al., 1990; Frankforter et al., 2010) and streams receiving wastewater effluent (Gücker et al., 2006). However, in a study of varying SRP and light levels in experimental flumes, Hill et al. (2009) determined that light was the more important factor limiting GPP. Even in the presence of adequate light, other factors such as herbivory (tropical stream in Puerto Rico; Ortiz-Zayas et al., 2005) and unstable substrates (sand-bed stream in Australia; Atkinson et al., 2008) can limit potential GPP. Although not studied with open-system methods, acidic conditions and toxic chemicals have also been shown to reduce GPP (see review by Young et al., 2008).

Two factors of great importance to ER are the longitudinal and lateral contributions of riparian or floodplain vegetation to the OM supply of the stream, and the vertical connectivity of the stream to the hyporheic zone. Generally, increased canopy cover in forested headwater streams provides a surplus of large woody debris (LWD) and a seasonal input of leaf litter to the stream that fuels heterotrophic activity (Mulholland et al., 2001, Acuña et al., 2004; McTammany et al., 2007; Roberts et al., 2007; Riley and Dodds, 2012). The RCC predicts that inefficient processing of OM upstream becomes important to downstream systems (Vannote et al., 1980), and OM input from the watershed or floodplain can stimulate ER (McTammany et al., 2003; Roberts et al., 2007). Even widening of the stream, which promotes greater GPP rates, can

be offset by dissolved OM from the floodplain or upstream sources (Edwards and Meyer, 1987; Meyer and Edwards, 1990).

In studying the vertical dynamics of stream-streambed exchange, many studies have used benthic chambers to assess the contribution of the hyporheic zone to ecosystem metabolism (e.g., Fellows et al., 2001), but a few important papers have used open-system metabolism methods to estimate the importance of the sub-sediment contributions to ER. Increased rates of ER have been found in streams with larger hyporheic or transient storage zones, with the latter including not only hyporheic exchange, but also side channels or eddies caused by LWD input (Mulholland et al., 1997; Mulholland et al., 2001). In one study, Grimm and Fisher (1987) used black plastic sheeting to cover a portion of the stream, thus treating the stream like a light-bottle, dark-bottle system. They determined that hyporheic respiration in a sandy, desert stream was almost enough to drive a traditionally autotrophic system to heterotrophy. Other factors affecting ER include temperature (Wiley et al., 1990), nutrients (Mulholland et al., 2001; Hall and Tank, 2003), and even autotrophic respiration (Wiley et al., 1990; McTammany et al., 2007; Townsend et al., 2011).

Floods have long been recognized as an important stream disturbance that can scour and/or displace algae and other organic matter, redistribute and disturb sediments, and alter the morphology of the stream (Peterson, 1996; Tank et al., 2010). Continual open-system studies in 6th order Swiss rivers and spates in a small forested stream in Tennessee have demonstrated how spates affect stream metabolism by depressing both primary production and ecosystem respiration (Uehlinger and Nageli, 1998; Uehlinger, 2000; Uehlinger, 2006; Roberts et al., 2007). These studies were important for several reasons, including the findings that spates affected GPP more than ER, driving the system towards net heterotrophy (decreasing P/R), and that recovery

of GPP was seasonally-specific, with increased sunlight in summer shortening recovery times. Likewise, Acuña et al. (2007) found that GPP recovery after storms was faster in spring prior to the canopy closure when more sunlight was able to reach the stream, again emphasizing the importance of light availability to increasing GPP rates. Acuña et al. (2007) also found out that ER recovery was mediated by benthic OM, with higher recovery rates in the fall after leaf excision. Conversely, Uehlinger (2006) found that there was no seasonal pattern of ER recovery related to storm frequency in large European rivers, which he attributed to a constant source of OM in the hyporheic zone that fueled ER, as opposed to lateral OM inputs characteristic of other similar sized streams. Floods can also affect stream GPP and ER by removing OM and opening spaces for algal colonization (Acuña et al., 2004), burying OM (Uehlinger, 2000; Houser et al., 2005), and uncovering previously buried OM (Metzler and Smock, 1990; Gerull et al., 2012).

In addition to their role in elucidating lotic function, open-system metabolism studies have also made significant contributions to the burgeoning database on land use effects on water quality. Several studies in streams flowing through agriculturally-dominated watersheds have reported high nutrient levels and GPP rates (Wiley et al., 1990; Young and Huryn, 1996; Izagirre et al., 2008), although excessive turbidity (e.g., cattle access to the stream) can reduce light availability and GPP (Hagen et al., 2010). Organic pollution from urban sources in the watershed has been associated with high ER rates (Bott et al., 2006; Izagirre et al., 2008), whereas watershed disturbances (e.g., deforestation or increased erosion) that result in a decreased amount of benthic OM and LWD in streams have been found to lower ER (Sweeney et al., 2004; Houser et al., 2005). Although the relationships between ecosystem metabolism rates and watershed land use metrics have been investigated, GPP and ER patterns have often been found to be stream-specific, making the detection of regional patterns difficult (Bernot et al.,

2010; Tank et al., 2010). However, in a large regional study across the U.S. and Puerto Rico, Bernot et al. (2010) were able to demonstrate predictable effects of watershed landscape variables (e.g., forest cover, agricultural and urban land use) on specific water chemistry and algal biomass characteristics of the stream, as well as GPP and ER.

Methodology

Open-system determinations of stream metabolism are based on monitoring diurnal increases in DO resulting from autotrophic primary production, and nocturnal declines caused by community respiration. Diffusion-based movement into and out of the stream (termed reaeration, k_2) must also be accounted for in stream metabolism calculations. Reaeration is dependent on turbulence, oxygen solubility, and water column DO concentrations, with oxygen diffusing out of the water if it is supersaturated, or into the water if DO saturation is less than 100%. Open-system studies (e.g., Young and Huryn, 1996) provide a more realistic assessment of whole-stream metabolism than can be achieved with microcosm-based experiments.

Although *in situ* microcosms have been used successfully to investigate specific factors that affect GPP and ER (e.g., substrate composition; Cardinale et al., 2002), isolating the study units from the stream eliminates the constant input of nutrients and dissolved gases, disturbs the substrate, and generally underestimates actual metabolism rates (Young et al., 2008).

Open-system metabolism measurements use either single-station or two-station approaches, both of which have their advantages and disadvantages. The single-station approach takes DO measurements at one position in the stream, assuming that DO concentrations and stream morphology are relatively homogeneous laterally and upstream of the reach. It is considered more economical, as only one monitoring device is deployed at each site and the

measurement of travel time not necessary. The two-station approach measures DO concentrations in a “parcel” of water as it moves from upstream to downstream stations, with changes in DO between the two stations attributed to GPP and ER. There is no assumption of homogeneity of the system upstream of the sensors, but accurate measurements of travel time between the stations are necessary. Young and Huryn (1999) reported that the two-station method was more effective in streams with more turbulent flows (e.g., incised channels, higher bed roughness) and low GPP rates, but in tranquil and productive streams, both methods worked well. Similarly, Edwards and Meyer (1987) found no differences in metabolism rates estimated with the two methods in a low-gradient, 6th-order stream.

The largest source of uncertainty in the application of open-system methods to stream metabolism studies is the calculation of reaeration (Mulholland et al., 2001), which can vary by estimation method but is also sensitive to hydrodynamic factors such as groundwater input (McCutchen et al., 2002) or heterogenous distribution of oxygen within the water column, especially in large rivers (Reichert et al., 2009). Reaeration can be estimated with a dissipation model (EDM) or surface renewal model (SRM), both of which are based on empirical equations that use some combination of stream velocity or discharge, depth, and/or slope of the channel (Bott, 2006; Aristegi et al., 2009). Alternatively, regressions of diurnal or nocturnal changes in oxygen concentration versus the saturation/deficit of DO based on the diel DO profile can be used to estimate k_{O_2} (Hornberger and Kelly, 1975; Kosinski, 1984). The nighttime regression, when significant (see Izagirre et al., 2008), method is the most frequently used approach and can be applied to previously recorded DO profiles. Reaeration can also be measured accurately with the concurrent injection of a conservative tracer (e.g., Cl^- or Br^-) and volatile gas (propane or SF_6) into the stream (Marzoff et al., 1994; Marzoff et al., 1999; Young and Huryn, 1999).

Mulholland et al. (2001) found that ko_2 calculated from empirical equations at shallow sites (<20 cm average depth) tended to underestimate reaeration values derived from tracer gas methods, which was also reported by Young and Huryn (1999) for turbulent streams with lots of cascades. However, empirical equations have been used successfully in many important studies of ecosystem metabolism or have been used in combination with other methods (e.g., McTammany et al., 2003; Sweeney et al., 2004; Ortiz-Zayas et al., 2005, Menninger et al., 2008), have correlated well with both nocturnal regressions (Aristegi et al., 2009) and tracer gas injections (Acuña et al. 2004; Ortiz-Zayas et al., 2005), and are easily calculated from simple hydrologic measurements (Bott, 2006). Although estimating ko_2 with nocturnal regression methods is based on the oxygen records for the stream and does not require hydrologic measurements such as stream velocity or depth, regressions are not always significant or of adequate fit (e.g., Izagirre et al., 2008). Additionally, Young and Huryn (1996) found that nocturnal regression methods did not work well when GPP rates were low or diffusion rates were high. Overall, the gas tracer method is considered to be the most accurate, but expensive equipment is necessary and techniques can be complicated (Young et al., 2008).

Scope

The next three chapters are research chapters using open-system methods of calculating ecosystem metabolism from diel dissolved oxygen curves in coastal plain streams of southeastern Louisiana. Chapter 2 discusses with a seasonal study in four streams, two with a closed canopy during summer months and 2 with an open canopy virtually year-round where the presence or absence of the canopy mediates both GPP and ER in the stream. Chapter 3 is a spatial snapshot of ecosystem metabolism rates during summer months at several streams

varying in size from 1st through 4th order and morphology, including shallow to deep streams and streams with a range of LWD. Chapter 4 describes a 2-year semi-continuous study at one site where unstable substrates shift with passing storms and affect both GPP and ER. Lastly, the final chapter summarizes my conclusions and includes suggestions for future research directions.

References

- Acuña, V., A. Giorgi, I. Muñoz, U. Uehlinger, and S. Sabater, 2004. Flow extremes and benthic organic matter shape the metabolism of a headwater Mediterranean stream. *Freshwater Biology* 49:960-971.
- Acuña, V., A. Giorgi, I. Muñoz, F. Sabater, and S. Sabater, 2007. Meteorological and riparian influences on organic matter dynamics in a forested Mediterranean stream. *Journal of the North American Benthological Society* 26:54-69.
- Aristegi, L., O. Izagirre, and A. Elosegi, 2009. Comparison of several methods to calculate reaeration in streams, and their effects on estimation of metabolism. *Hydrobiologia* 635:113-124.
- Atkinson, B.L., M.R. Grace, B.T. Hart, and K.E.N. Vanderkruk, 2008. Sediment instability affects the rate and location of primary production and respiration in a sand-bed stream. *Journal of the North American Benthological Society* 27:581-592.
- Bernot, M.J., D.J. Sobota, R.O. Hall, P.J. Mulholland, W.K. Dodds, J.R. Webster, J.L. Tank, L.R. Ashkenas, L.W. Cooper, C.N. Dahm, S. Findlay, S.V. Gregory, N.B. Grimm, S.K. Hamilton, S.L. Johnson, W.H. McDowell, J.L. Meyer, B.J. Peterson, G.C. Poole, H.M. Valett, C. Arango, J.J. Beaulieu, A.J. Burgin, C. Crenshaw, A.M. Helton, L. Johnson, J. Merriam, B.R. Niederlehner, J.M. O'Brien, J.D. Potter, R.W. Sheibley, S.M. Thomas, and K. Wilson, 2010. Inter-regional comparison of land-use effects on stream metabolism. *Freshwater Biology* 55:1874-1890.
- Bott, T.L., 2006. Primary production and community respiration. In: Hauer, F.R., and G.A. Lamberti, (editors), *Methods in Stream Ecology*, 2nd edition. Academic Press, Burlington, MA: 663-690.
- Bott, T.L., D.S. Montgomery, J.D. Newbold, D.B. Arscott, C.L. Dow, A.K. Aufdenkampe, J.K. Jackson, and L.A. Kaplan, 2006. Ecosystem metabolism in stream of the Catskill Mountains (Delaware and Hudson River watersheds) and Lower Hudson Valley. *Journal of the North American Benthological Society* 25:1018-1044.

- Cardinale, B.J., M.A. Palmer, C.M. Swan, S. Brooks, and N.L. Poff, 2002. The influence of substrate heterogeneity on biofilm metabolism in a stream ecosystem. *Ecology* 83:412-422.
- Dodds, W.K., R.E. Hutson, A.C. Eichen, M.A. Evans, D.A. Gudder, K.M. Fritz, and L. Gray, 1996. The relationship of floods, drying, flow and light to primary production and producer biomass in a prairie stream. *Hydrobiologia* 333:151-159.
- Edwards, R.T., and J.L. Meyer, 1987. Metabolism of a sub-tropical low gradient blackwater river. *Freshwater Biology* 17:251-263.
- Fellows, C.S., H.M. Valett, and C.N. Dahm, 2001. Whole-stream metabolism in two montane streams: contribution of the hyporheic zone. *Limnology and Oceanography* 46:523-531.
- Fellows, C.S., J.E. Clapcott, J.W. Udy, S.E. Bunn, B.D. Harch, M.J. Smith, and P.M. Davies, 2006. Benthic metabolism as an indicator of stream ecosystem health. *Hydrobiologia* 572:71-87.
- Fisher, S.G., L.J. Gray, N.B. Grimm, and D.E. Busch, 1982. Temporal succession in a desert stream ecosystem following flash flooding. *Ecological Monographs* 52:93-110.
- Frankforter, J.D., H.S. Weyers, J.D. Bales, P.W. Moran, and D.L. Calhoun, 2010. The relative influence of nutrients and habitat on stream metabolism in agricultural streams. *Environmental Monitoring and Assessment* 168:461-479.
- Gerull, L., A. Frossard, M.O. Gessner, and M. Mutz, 2012. Effects of shallow and deep sediment disturbance on whole-stream metabolism in experimental sand-bed flumes. *Hydrobiologia* 683:297-310.
- Grimm, N.B., and S.G. Fisher, 1987. Exchange between interstitial and surface water: implications for stream metabolism and nutrient cycling. *Hydrobiologia* 111:219-228.
- Gücker, B., M. Brauns, and M.T. Pusch, 2006. Effects of wastewater treatment plant discharge on ecosystem structure and function of lowland streams. *Journal of the North American Benthological Society* 25:313-329.
- Hagen, E.M., M.E. McTammany, J.R. Webster, and E.F. Benfield, 2010. Shifts in allochthonous input and autochthonous production in stream along an agricultural land-use gradient. *Hydrobiologia* 655:61-77.
- Hall, R.O., and J.L. Tank, 2003. Ecosystem metabolism controls nitrogen uptake in streams in Grand Teton National Park, Wyoming. *Limnology and Oceanography* 48:1120-1128.
- Hill, W.R., P.J. Mulholland, and E.R. Marzolf, 2001. Stream ecosystem responses to forest leaf emergence in spring. *Ecology* 82:2306-2319.

- Hill, W.R., S.E. Fanta, and B.J. Roberts, 2009. Quantifying phosphorus and light effects in stream algae. *Limnology and Oceanography* 54:368-380.
- Hornberger, G.M., and M.G. Kelly, 1975. Atmospheric reaeration in a river using productivity analysis. *Journal of the Environmental Engineering Division-ASCE* 101:729-739.
- Houser, J.N., P.J. Mulholland, and K.O. Maloney, 2005. Catchment disturbance and stream metabolism: patterns in ecosystem respiration and gross primary production along a gradient of upland soil and vegetation disturbance. *Journal of the North American Benthological Society* 24:538-552.
- Izagirre, O., U. Agirre, M. Bermejo, J. Pozo, and A. Elosegi, 2008. Environmental controls of whole-stream metabolism identified from continuous monitoring of Basque streams. *Journal of the North American Benthological Society* 27:252-268.
- Kosinski, R.J., 1984. A comparison of the accuracy and precision of several open-water oxygen productivity techniques. *Hydrobiologia* 119:139-148.
- Lamberti, G.A., and A.D. Steinman, 1997. A comparison of primary production in stream ecosystems. *Journal of the North American Benthological Society* 16:95-104.
- Larned, S.T., 2010. A prospectus for periphyton: recent and future ecological research. *Journal of the North American Benthological Society* 29:182-206.
- Marzolf, E.R., P.J. Mulholland, and A.D. Steinman, 1994. Improvements to the diurnal upstream-downstream dissolved oxygen change technique for determining whole-stream metabolism in small streams. *Canadian Journal of Fisheries and Aquatic Sciences* 51:1591-1599.
- Marzolf, E.R., P.J. Mulholland, and A.D. Steinman, 1998. Reply: improvements to the diurnal upstream-downstream dissolved oxygen change technique for determining whole-stream metabolism in small streams. *Canadian Journal of Fisheries and Aquatic Sciences* 55:1786-1787.
- McCutchan, J.H., J.F. Saunders, W.M. Lewis, Jr., and M.G. Hayden, 2002. Effects of groundwater flux on open-channel estimates of stream metabolism. *Limnology and Oceanography* 47:321-324.
- McTammany, M.E., J.R. Webster, E.F. Benfield, and M.A. Neatrour, 2003. Longitudinal patterns of metabolism in a southern Appalachian river. *Journal of the North American Benthological Society* 22:359-370.
- McTammany, M.E., E.F. Benfield, and J.R. Webster, 2007. Recovery of stream ecosystem metabolism from historical agriculture. *Journal of the North American Benthological Society* 26:532-545.

- Menninger, H.L., M.A. Palmer, L.S. Craig, and D.C. Richardson, 2008. Periodical cicada detritus impacts stream ecosystem metabolism. *Ecosystems* 11:1306-1317.
- Metzler, G.M., and L.A. Smock, 1990. Storage and dynamics of subsurface detritus in a sand-bottomed stream. *Canadian Journal of Fisheries and Aquatic Sciences* 47:588-594.
- Meyer, J.L., and R.T. Edwards, 1990. Ecosystem metabolism and turnover of organic carbon along a blackwater river continuum. *Ecology* 71:668-677.
- Minshall, G.W., 1978. Autotrophy in stream ecosystems. *Bioscience* 28:767-771.
- Minshall, G.W., R.C. Petersen, K.W. Cummins, T.L. Bott, J.R. Sedell, C.E. Cushing, and R.L. Vannote, 1983. Interbiome comparison of stream ecosystem dynamics. *Ecological Monographs* 53:1-25.
- Mulholland, P.J., E.R. Marzolf, J.R. Webster, D.R. Hart, and S.P. Hendricks, 1997. Evidence that hyporheic zones increase heterotrophic metabolism and phosphorus uptake in forest streams. *Limnology and Oceanography* 42:443-451.
- Mulholland, P.J., C.S. Fellows, J.L. Tank, N.B. Grimm, J.R. Webster, S.K. Hamilton, E. Marti, L. Ashkenas, W.B. Bowden, W.K. Dodds, W.H. McDowell, M.J. Paul, and B.J. Peterson, 2001. Inter-biome comparison of factors controlling stream metabolism. *Freshwater Biology* 46:1503-1517.
- Odum, H.T., 1956. Primary production in flowing waters. *Limnology and Oceanography* 1:103-117.
- Odum, H.T., 1957. Trophic structure and productivity of Silver Springs, Florida. *Ecological Monographs* 27:55-112.
- Ortiz-Zayas, J.R., W.M. Lewis, Jr., J.F. Saunders, J.H. McCutchan, and F.N. Scantena, 2005. Metabolism of tropical rainforest stream. *Journal of the North American Benthological Society* 24:769-783.
- Peterson, C.G., 1996. Response of benthic algal communities to natural physical disturbance. In: Stevenson, R. J., M.L., Bothwell, and R.L. Lowe (editors). *Algal Ecology: Freshwater Benthic Ecosystems*. San Diego, Academic Press: 375-402.
- Reichert, P., U. Uehlinger, and V. Acuna, 2009. Estimating stream metabolism from oxygen concentrations: effect of spatial heterogeneity. *Journal of Geophysical Research-Biogeosciences* 114. doi:10.1029/2008JG000917.
- Riley, A.J., and W.K. Dodds, 2012. The expansion of woody riparian vegetation, and subsequent stream restoration, influences the metabolism of prairie streams. *Freshwater Biology* 57:1138-1150.

- Roberts, B.J., P.J. Mulholland, and W.R. Hill, 2007. Multiple scales of temporal variability in ecosystem metabolism rates: results from 2 years of continuous monitoring in a forested headwater stream. *Ecosystems* 10:588-606.
- Sweeney, B.W., T.L. Bott, J.K., Jackson, L.A. Kaplan, J.D. Newbold, L.J. Standley, W.C. Hession, and R.J. Horwitz, 2004. Riparian deforestation, stream narrowing, and loss of stream ecosystem services. *Proceedings of the National Academy of Sciences* 101:14132-14137.
- Tank, J.L., E.J. Rosi-Marshall, N.A. Griffiths, S.A. Entekin, and M.L. Stephen, 2010. A review of allochthonous organic matter dynamics and metabolism in streams. *Journal of the North American Benthological Society* 29:118-146.
- Townsend, S.A., I.T. Webster, and J.H. Schult, 2011. Metabolism in groundwater-fed river system in the Australian wet/dry tropics: tight coupling of photosynthesis and respiration. *Journal of the North American Benthological Society* 30:603-620.
- Uehlinger, U., and M.W. Naegeli, 1998. Ecosystem metabolism, disturbance, and stability in a prealpine gravel bed river. *Journal of the North American Benthological Society* 17:165-178.
- Uehlinger, U., 2000. Resistance and resilience of ecosystem metabolism in a flood-prone river system. *Freshwater Biology* 45:319-332.
- Uehlinger, U., 2006. Annual cycle and inter-annual variability of gross primary production and ecosystem respiration in a flood-prone river during a 15-year period. *Freshwater Biology* 51:938-950.
- Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell, and C.E. Cushing, 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37:130-137.
- Wiley, M.J., L.L. Osborne, and R.W. Larimore, 1990. Longitudinal structure of an agricultural prairie river system and its relationship to current stream ecosystem theory. *Canadian Journal of Fisheries and Aquatic Sciences* 47:373-384.
- Young, R.G., and A.D. Huryn, 1996. Interannual variation in discharge controls ecosystem metabolism along a grassland river continuum. *Canadian Journal of Fisheries and Aquatic Sciences* 53:2199-2211.
- Young, R.G., and A.D. Huryn, 1998. Comment: improvements to the diurnal upstream-downstream dissolved oxygen change technique for determining whole-stream metabolism in small streams. *Canadian Journal of Fisheries and Aquatic Sciences* 55:1784-1785.
- Young, R.G., and A.D. Huryn, 1999. Effects of land use on stream metabolism and organic matter turnover. *Ecological Applications* 9:1359-1376.

Young, R.G., C.D. Matthaei, and C.R. Townsend, 2008. Organic matter breakdown and ecosystem metabolism: functional indicators for assessing river ecosystem health. *Journal of the North American Benthological Society* 27:605-625.

CHAPTER 2. SEASONAL VARIATION IN STREAM METABOLISM IN SHADED AND UNSHADED SAND-BOTTOM STREAMS OF THE SOUTHEASTERN LOUISIANA COASTAL PLAIN

Introduction

Stream metabolism, a combination of gross primary production (GPP) and ecosystem respiration (ER), helps describe the derivation and processing of organic matter (OM) in lotic ecosystems. Within streams, photoautotrophic benthic algae produce organic carbon during GPP with oxygen as a byproduct. In contrast, lotic ER uses oxygen during consumption of organic carbon within the stream. As such, GPP and ER rates in streams can be calculated using diel dissolved oxygen (DO) curves, with the ratio or difference between these two rates indicating whether the organic carbon is produced autochthonous (net autotrophic) or allochthonous (net heterotrophic) the system. As methods have become more refined (Marzolf et al., 1994), an increased number of studies from various regions have elucidated general patterns in stream production and respiration, and it has been suggested that metabolism rates can provide a functional assessment of stream health (Fellows et al., 2006; Young et al., 2010).

Both components of stream metabolism are influenced by several factors that vary both temporally and spatially. GPP is stimulated by increased light, which can vary seasonally with leaf abscission from riparian canopies or angles of incident sunlight in summer months, or by increased nutrients, which can vary regionally through geography or anthropogenic inputs (Wiley et al., 1990; Young and Huryn, 1996; Young and Huryn, 1998; Hill et al., 2001; Mulholland et al., 2001; Bernot et al., 2008). Likewise, GPP is suppressed by grazing (e.g., Rosemond et al., 1993; Acuña et al., 2004; Ortiz-Zayas et al., 2005) or disturbance events such as floods that can cause sediment instability, increased turbidity, and benthic scouring or burial of algae (Uehlinger and Naegeli, 1998; Uehlinger, 2000; Atkinson et al., 2008). GPP can also be

stimulated during flooding through the removal of leaves or other organic debris (e.g., Acuña et al., 2004; Roberts et al., 2007). Stream ER can be stimulated by OM input, including downstream transport of dissolved and particulate OM, large woody debris (LWD) and leaf litter input from the catchment and riparian canopy, as well as autotrophic production by algae (Meyer and Edwards, 1990; Young and Huryn, 1999; McTammany et al., 2007; Roberts et al., 2007). In turn, disturbances can flush OM from the system, possibly decreasing ER rates (Acuña et al., 2004; Houser et al., 2005). Each of these factors can act alone or in concert to affect the net autotrophic or heterotrophic status of a stream (Young et al., 2008).

Many small Louisiana streams (1st to 2nd order) tend to be either turbid or brown-stained, slow-moving, stagnant systems rich in OM and nutrients that often exhibit persistent hypoxia from high rates of decomposition. However, as stream size increases (>2nd order), many of these streams are found in wider valleys with relatively faster flows, sandier substrates, and clearer water, suggesting conditions favorable for increased primary production by stream algae. I investigated temporal patterns of GPP and ER in shaded (2nd order) and unshaded (3rd order) Louisiana streams, hypothesizing that: 1) shaded streams would exhibit lower GPP rates than unshaded streams due to increased light interception by the riparian canopy and higher ER from leaf litter input; 2) these streams would remain heterotrophic throughout the year because of their high OM load and minimal flushing; and 3) unshaded streams would have comparatively high rates of GPP and become autotrophic during summer due to increased light and clear water, especially in a stream with higher ambient nutrient concentrations.

Methods and Materials

This study was conducted seasonally over two years in four streams within the southeastern Plains and Mississippi Valley Loess Plains ecoregions of southeastern Louisiana where landuse patterns in the watersheds are typically forested with some upland agriculture (Fig. 1). Each of the study sites was characterized by sand-dominated substrates, clear water, and low to moderate gradients resulting in low stream velocities, generally laminar stream flow, and relatively little turbulence (Folley, 1992). Tchefuncte Creek (TCH) and Boguelusa Creek (BGL) are 2nd order streams that have a more incised channel and rarely inundate their floodplains at the study reaches. Consequently, these streams have more intact riparian canopies that provide shade and a considerable supply of large woody debris (LWD) and leaf litter to the stream (Table 1). In contrast, West Fork of Thompson Creek (WFT) and Darling Creek (DRL) are 3rd order streams that have flashier hydrographs and maintain a set-back riparian canopy due to the scouring of vegetation and sediments from the side of the stream channel areas during spates, resulting in the an open stream canopy. These two unshaded systems have much less woody debris and leaf litter input, and have much less stable habitats, i.e., loose woody debris that is not wedged into the stream edge or partially buried in the sediments is usually washed downstream during storm events. For the rest of this paper, BGL and TCH are classified as shaded streams while WFT and DRL are unshaded streams.

My sampling scheme was seasonal, with all samples collected when streams were as close to baseflow conditions as possible. Prior nutrient sampling led to *a priori* classification of TCH and WFT as higher nutrient streams, with BGL and DAR characterized by lower nutrient concentrations (D.G. Kelly, LSU AgCenter, unpublished data). I attempted to find study sites within each stream that were of similar width and depth. Prior to sampling, I measured

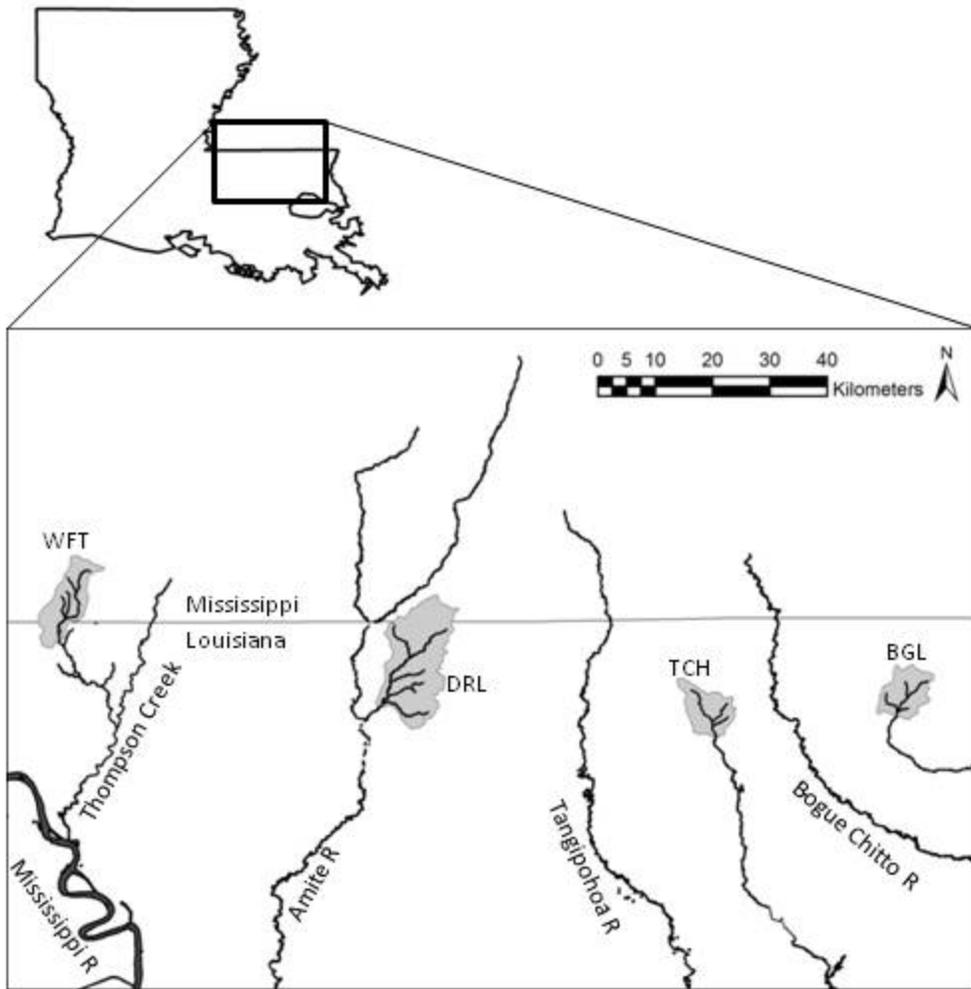


Fig. 1 Location of watersheds and the study streams in southeastern Louisiana. The most downstream boundary of the watershed represents the location of the datasondes.

temperature, specific conductance, dissolved oxygen (DO) concentration and % saturation, pH, and turbidity with a YSI 6820 V2 multiparameter water quality sonde (YSI Incorporated; Yellow Springs, OH). DO for this sonde was measured with a Clark sensor that was calibrated in water-saturated air approximately weekly. Triplicate water samples were collected in acid-washed, brown 125 mL HDPE Nalgene bottles, placed on ice for transport, stored at 4°C, filtered with

Table 1 Characteristics of the study streams located in the coastal plain of southeastern Louisiana. Watershed size and slope were calculated with USGS digital elevation models.

Stream Name	Abbreviation	Order	Canopy Cover	Watershed Size (hectares)	Slope (m/m)
<i>Shaded Streams</i>					
Boguelusa Creek	BGL	2nd	High	5210.40	0.00208
Tchefuncte Creek	TCH	2nd	High	5109.96	0.00130
<i>Unshaded Streams</i>					
West Fork of Thompson Creek	WFT	3rd	Low	6903.01	0.00245
Darling Creek	DRL	3rd	Low	16874.19	0.00192

Whatman 0.45- μm glass microfiber filters, and analyzed within 24 hrs of collection for nitrate ($\text{NO}_3\text{-N}$), ammonium ($\text{NH}_4\text{-N}$), and orthophosphate ($\text{PO}_4\text{-P}$; APHA, 2005) with a Hach DR/2500 spectrophotometer.

Within each stream, morphology was quantified within a 100-m reach that was randomly selected >200 m upstream of the site access point. I used the line-transect method (Wallace and Benke, 1984) to measure wetted width, stream depth (3 per transect), and large woody debris (LWD) abundance along ten evenly spaced transects within the reach placed perpendicular to the stream channel across the stream. I also visually estimated percent algal cover within a 50-cm band along both sides of each transect (Lewis and Taylor, 1967). In the middle of each transect, I photographed canopy cover with a Kodak EasyShare Z740 camera fitted with an orthographic Opteka fish-eye lens ~1 m above the stream, with percent canopy openness estimated with Gap Light Analyzer v. 2 (Frazer et al., 1999). Stream discharge was measured at the top, bottom, and middle of the reach with a YSI SonTek FlowTracker Handheld Acoustic Doppler Velicometer (YSI Incorporated; Yellow Springs, OH) based on the cross-sectional area method (Gordon et al., 2004), and I used a NaCl slug injection to double-check discharge and to estimate stream velocity (Gordon et al., 2004). Channel slope and stream order were taken from United States

Geological Survey digital elevation models (<http://atlas.lsu.edu> and <http://www.maris.state.ms.us>). I also collected the upper 10 cm of stream sediment with a 10.1-cm diameter PVC tube (81.7 cm² area) at 5 random spots within the reach for analysis of benthic organic matter (BOM). Sediment samples were homogenized, subsampled, dried for at least 48 hours at 103°C, and placed in a muffle furnace at 550°C for 4 hours to determine ash free dry mass (AFDM) and percent BOM content.

GPP and ER were calculated from diel dissolved oxygen curves for three consecutive days per sampling period as $\Delta\text{DO} = \text{GPP} + \text{ER} + k(C_s - C)$, where ΔDO is the dissolved oxygen change per time step, k is the reaeration coefficient, C is the DO concentration, and C_s is the DO concentration at saturation given the ambient temperature (Bott, 2006). At night, GPP is zero, thus the equation becomes $\Delta\text{DO} = \text{ER} + k(C_s - C)$, with ER rates extrapolated over the diurnal period. I measured DO, % saturation, temperature, and water depth every 15 minutes during each sampling period with a YSI 6600EDS-S extended deployment water quality datasonde (Yellow Springs, OH). I also measured DO, % saturation, and temperature prior to datasonde deployment and upon retrieval with a YSI 6820 water quality monitor to test for and correct instrument drift and/or fouling. Stream reaeration was estimated with the energy dissipation model (EDM, Tsvoglou and Neal, 1976) as $k' \times \text{velocity} \times \text{slope}$, where the reaeration constant k' varies as a function of stream discharge (Bott, 2006). Reaeration values were converted to 15 minute intervals and corrected for temperature (Elmore and West, 1961).

Daily total solar radiation (in W m^{-2}) data were collected from Louisiana Agriclimate Information System sites (<http://weather.lsuagcenter.com/>). I used data from the Southeast Research Station in Franklinton for Boguelusa Creek and the Tchefuncte River, and the LIGO Corner Research Station in Livingston for West Fork of Thompson and Darling creeks. At each

station, solar radiation was measured with a LiCor 200x pyranometer and logged with a Campbell Scientific CR23x. Data were converted to photosynthetically active radiation (PAR) according to McCree (1972). Barometric pressure data were taken from the nearest US Weather Service stations to each of the study sites and were used to verify datasonde % DO saturation data.

Differences between shaded and unshaded streams and among seasonal and yearly rates of GPP, ER, and percent BOM (logit transformed) at each site were analyzed via 3-way analysis of variance (ANOVA) with PROC GLM and Tukey's post hoc pairwise comparisons in SAS 9.3 (SAS, 2011). Differences in LWD among sites were tested with a one-way ANOVA and a Tukey's post hoc test. I used PROC REG to estimate the regression slopes of PAR on GPP for shaded and unshaded sites and compared the slopes between the sites with an analysis of covariance (ANCOVA; PROC GLM, SAS, 2011).

Results

Specific conductance and pH tended to be highest in WFT throughout the study period, with uniformly high DO ($> 6 \text{ mg l}^{-1}$) for most of the streams, particularly during fall and winter (Table 2). Temperature at all sites tended to vary according to season, with higher temperatures in spring and summer and lower temperatures in fall and winter. Turbidity varied with recent storm activity, but was usually low ($< 10 \text{ NTUs}$), particularly in summer and fall. Water velocities and discharge rates usually peaked in the winter and spring (Table 3), and were typically highest in DRL. Reaeration (k_{O_2}) ranged from $3.28 - 23.19 \text{ day}^{-1}$ and tended to be relatively low in these slow, nearly laminar-flowing streams. Reaeration coefficients calculated with nighttime regression rates (see Hornberger and Kelly, 1975) were consistent with reaeration

Table 2 Physicochemical characteristics of the study streams during the seasonal 3-day sampling periods recorded by a YSI-6600EDS-S extended deployment datasonde. Data presented are mean (\pm SD).

Year	Season	Stream	Specific Conductance ($\mu\text{S cm}^{-1}$)	Dissolved Oxygen (mg l^{-1})	Temperature ($^{\circ}\text{C}$)	pH	Turbidity (NTU)
2007	Winter	BGL	52 (1)	9.88 (0.30)	10.80 (0.81)	6.0 (0.02)	2.6 (1.1)
		TCH	56 (5)	9.39 (0.34)	11.32 (0.78)	6.0 (0.06)	33.3 (7.3)
		WFT	78 (10)	11.66 (0.65)	8.03 (0.81)	6.6 (0.09)	20.9 (8.0)
		DRL					
	Spring	BGL	28 (1)	7.84 (0.65)	20.85 (1.21)	5.8 (0.04)	5.8 (3.1)
		TCH	46 (1)	7.54 (0.57)	20.32 (0.96)	6.0 (0.02)	23.1 (15.5)
		WFT	130 (5)	8.70 (0.70)	23.73 (2.03)	6.7 (0.07)	20.1 (5.0)
		DRL					
	Summer	BGL	23 (2)	6.41 (1.21)	24.27 (0.81)	5.6 (0.07)	1.2 (0.4)
		TCH	36 (3)	6.32 (0.41)	22.77 (0.52)	6.0 (0.06)	2.3 (1.1)
		WFT	87 (3)	7.42 (1.17)	29.84 (2.73)	7.5 (0.66)	9.4 (3.0)
		DRL	25 (3)	8.46 (0.53)	25.02 (1.36)	6.4 (0.24)	14.6 (9.2)
	Fall	BGL	23 (1)	9.56 (0.42)	13.64 (1.58)	5.3 (0.04)	2.8 (0.4)
		TCH	35 (1)	8.17 (0.50)	15.68 (1.35)	5.4 (0.03)	7.6 (1.1)
		WFT	90 (1)	9.48 (1.01)	19.66 (1.21)	7.6 (0.65)	2.7 (0.6)
		DRL	33 (0.3)	8.98 (0.61)	18.84 (1.09)	5.9 (0.08)	1.8 (0.3)
2008	Winter	BGL	26 (1)	8.30 (0.38)	15.31 (1.51)	5.4 (0.07)	3.7 (7.3)
		TCH	52 (1)	7.75 (0.41)	15.30 (0.88)	5.6 (0.04)	15.3 (5.6)
		WFT	75 (1)	10.59 (0.55)	13.73 (2.52)	6.1 (0.38)	24.6 (8.3)
		DRL	31 (2)	10.59 (1.17)	12.59 (1.23)	5.9 (0.05)	19.4 (3.3)
	Spring	BGL	27 (0.2)	5.84 (0.16)	24.53 (0.79)	6.4 (0.04)	9.5 (7.1)
		TCH	46 (1)	6.46 (0.40)	23.08 (0.56)	5.3 (0.04)	9.0 (7.6)
		WFT	85 (31)	8.41 (0.81)	26.86 (2.74)	7.8 (0.36)	7.8 (3.7)
		DRL	35 (1)	9.62 (3.89)	25.62 (2.54)	6.7 (0.18)	2.1 (3.8)
	Summer	BGL	27 (2)	7.18 (0.37)	24.72 (0.73)	5.5 (0.07)	1.3 (0.7)
		TCH	49 (9)	5.78 (0.42)	23.54 (0.39)	5.5 (0.08)	2.0 (4.5)
		WFT	118 (2)	7.81 (0.99)	27.25 (1.81)	7.6 (0.24)	38.9 (5.6)
		DRL	45 (1)	8.13 (0.93)	24.59 (1.03)	6.0 (0.09)	6.4 (1.2)
	Fall	BGL	32 (1)	8.23 (0.20)	15.67 (0.82)	5.7 (0.06)	1.5 (0.5)
		TCH	61 (2)	7.09 (0.23)	16.85 (0.61)	5.7 (0.03)	5.2 (5.1)
		WFT	139 (2)	9.07 (0.63)	10.09 (2.24)	7.6 (0.17)	1.8 (0.4)
		DRL	49 (0.3)	10.96 (0.39)	10.85 (1.30)	6.1 (0.09)	1.2 (0.5)

values calculated via EDM equations (data not shown; Pearson correlation: $r = 0.71$, $p < 0.01$, $n = 26$; non-significant nighttime regressions not used, see Izagirre et al., 2008).

Between the two shaded streams, TCH tended to have higher $\text{NO}_3\text{-N}$ and $\text{PO}_4\text{-P}$ concentrations than BGL while both systems tended to have high $\text{NH}_4\text{-N}$ concentrations (Table 3; Fig. 2a). Seasonally for both shaded streams, higher $\text{PO}_4\text{-P}$ concentrations occurred in spring

Table 3 Stream velocity and discharge measured seasonally with NaCl slug injection in the study streams. Width was the average wetted width on 10 transects and depth was measured at 30 points (3 per transect) within the 100-meter study reach. Reaeration (k_{O_2}) was calculated with the energy dissipation model (EDM). Nutrient concentrations are presented as the mean (\pm SD) and were collected prior to YSI installation.

Year	Season	Stream	Velocity ($m\ s^{-1}$)	Discharge ($m^3\ s^{-1}$)	Depth (m)	Width (m)	K_{O_2} (day^{-1})	NO_3-N ($mg\ l^{-1}$)	NH_4-N ($mg\ l^{-1}$)
2007	Winter	BGL	0.15	0.57	0.644	6.40	4.62	0.01 (0.001)	0.27 (0.023)
		TCH	0.21	0.56	0.416	8.40	12.31	0.36 (0.035)	0.17 (0.006)
		WFT	0.44	0.56	0.224	7.97	23.19	0.08 (0.009)	0.43 (0.006)
		DRL							
	Spring	BGL	0.06	0.14	0.498	5.05	3.28	0.01 (0.002)	0.26 (0.017)
		TCH	0.15	0.29	0.290	7.23	4.15	0.37 (0.035)	0.32 (0.015)
		WFT	0.16	0.17	0.180	7.12	11.09	0.06 (0.004)	0.14 (0.007)
		DRL							
	Summer	BGL	0.06	0.14	0.486	5.10	3.48	0.02 (0.001)	0.19 (0.006)
		TCH	0.19	0.28	0.319	6.50	5.18	0.25 (0.036)	0.24 (0.006)
		WFT	0.08	0.12	0.286	6.83	5.81	0.01 (0.001)	0.12 (0.009)
		DRL	0.23	0.55	0.319	11.23	9.38	0.01 (0.003)	0.11 (0.019)
	Fall	BGL	0.08	0.16	0.539	5.62	4.78	0.01 (0.003)	0.17 (0.007)
		TCH	0.11	0.31	0.469	7.60	4.01	0.25 (0.007)	0.20 (0.003)
		WFT	0.16	0.09	0.182	5.36	11.19	0.02 (0.004)	0.09 (0.003)
		DRL	0.20	0.39	0.314	10.71	8.00	0.01 (0.001)	0.03 (0.003)
2008	Winter	BGL	0.05	0.15	0.471	4.97	2.95	0.01 (0.001)	0.24 (0.010)
		TCH	0.16	0.28	0.469	8.74	4.43	0.15 (0.011)	0.26 (0.003)
		WFT	0.31	0.42	0.210	7.46	16.31	0.04 (0.003)	0.57 (0.007)
		DRL	0.25	0.55	0.324	11.54	10.02	0.01 (0.008)	0.62 (0.003)
	Spring	BGL	0.06	0.13	0.465	5.22	3.28	0.02 (0.0003)	0.17 (0.012)
		TCH	0.18	0.34	0.287	7.96	4.86	0.23 (0.016)	0.16 (0.015)
		WFT	0.30	0.3	0.216	7.12	15.81	0.01 (0.001)	0.20 (0.007)
		DRL	0.19	0.57	0.380	11.87	5.58	0.28 (0.010)	0.15 (0.009)
	Summer	BGL	0.06	0.14	0.429	5.12	3.39	0.01 (0.002)	0.19 (0.009)
		TCH	0.18	0.23	0.336	7.17	6.66	0.24 (0.010)	0.18 (0.003)
		WFT	0.18	0.11	0.152	6.04	12.18	0.02 (0.002)	0.21 (0.007)
		DRL	0.22	0.48	0.411	11.81	8.78	0.02 (0.005)	0.38 (0.026)
	Fall	BGL	0.06	0.21	0.557	5.45	3.60	0.01 (0.005)	0.12 (0.007)
		TCH	0.17	0.26	0.370	7.46	6.18	0.29 (0.013)	0.11 (0.012)
		WFT	0.18	0.15	0.203	6.18	11.58	0.01 (0.005)	0.12 (0.006)
		DRL	0.14	0.59	0.340	10.66	4.17	0.01 (0.003)	0.15 (0.012)

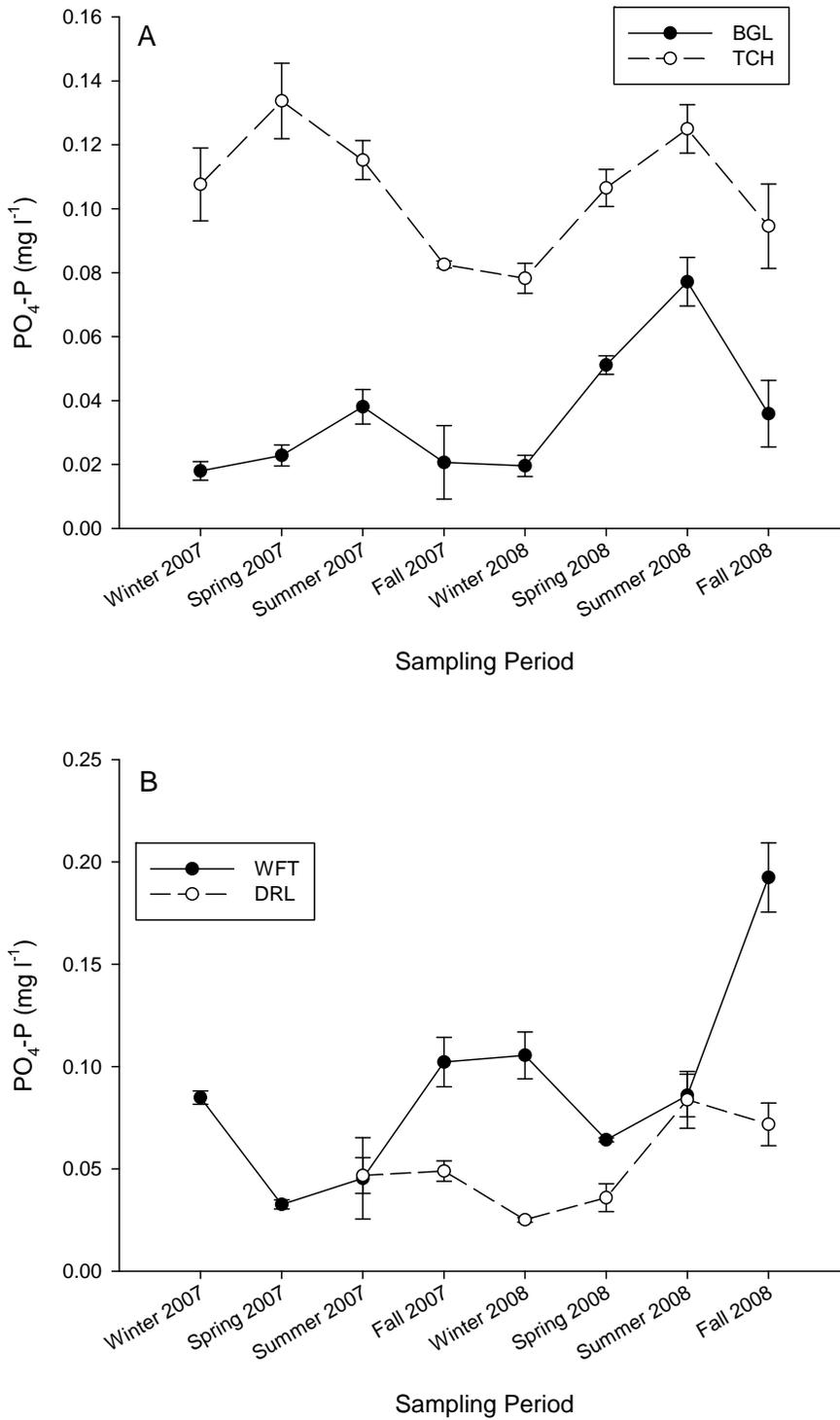


Fig. 2 Seasonal trends in ambient PO₄-P concentrations for (a) shaded and (b) unshaded sites in the four study streams in southeastern Louisiana.

and summer and lower concentrations in fall and winter (Fig. 2a). Dissolved inorganic nitrogen (DIN; $\text{NO}_3\text{-N} + \text{NH}_4\text{-N}$) concentrations were mostly a function of ambient ammonium and did not show any seasonal patterns (Fig. 3a). The opposite was true for unshaded streams where concentrations of nutrients either peaked at different seasons or were not evident (Table 3; Fig. 2b). Additionally, DIN concentrations exhibited similar concentrations and seasonal patterns in unshaded streams, being highest during winter and lowest in the fall for both streams (Fig. 3b).

Mean GPP rates in all streams ranged from $0.14 - 4.61 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$, with unshaded streams exhibiting rates that were about two-fold higher than shaded streams during summer months (Fig. 4a). For both of the shaded streams, the lowest GPP rates occurred in spring and fall 2008, while in the two unshaded streams, GPP rates were consistently high in spring and summer, and lowest in the fall for both years. ER rates ranged from $0.24 - 9.60 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$, with an overall mean of $3.56 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ at all sites throughout the study period, with shaded streams tending to have higher ER rates than unshaded streams (Fig. 4b). In shaded streams, ER rates peaked in the fall, coincident with leaf litter inputs following fall leaf senescence. In contrast, annual or seasonal trends in ER rates in unshaded streams were not apparent, with the highest rates recorded in fall 2008 at one site when leaf litter densities were highest in the stream during the fall sampling period (Fig. 4b). Tukey's pairwise differences among shaded versus unshaded streams, seasons, years, and all interactions were significant at $p < 0.01$ for both GPP and ER (see Appendix Table A2.1 and A2.1). Net ecosystem production (NEP), the difference between GPP and ER, was negative for all sites except DRL in summer 2007 and 2008.

PAR was positively associated with GPP in unshaded streams ($R^2 = 0.39$; $p < 0.01$; $n = 42$), but not in shaded streams ($R^2 = 0.004$, $p = 0.68$; $n = 48$; Fig. 5). In fact, the highest GPP

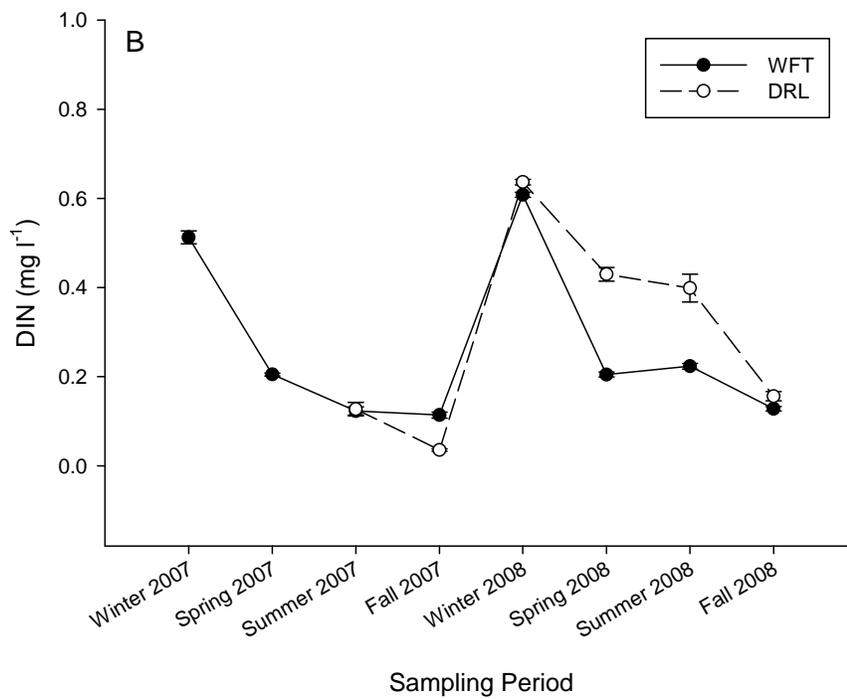
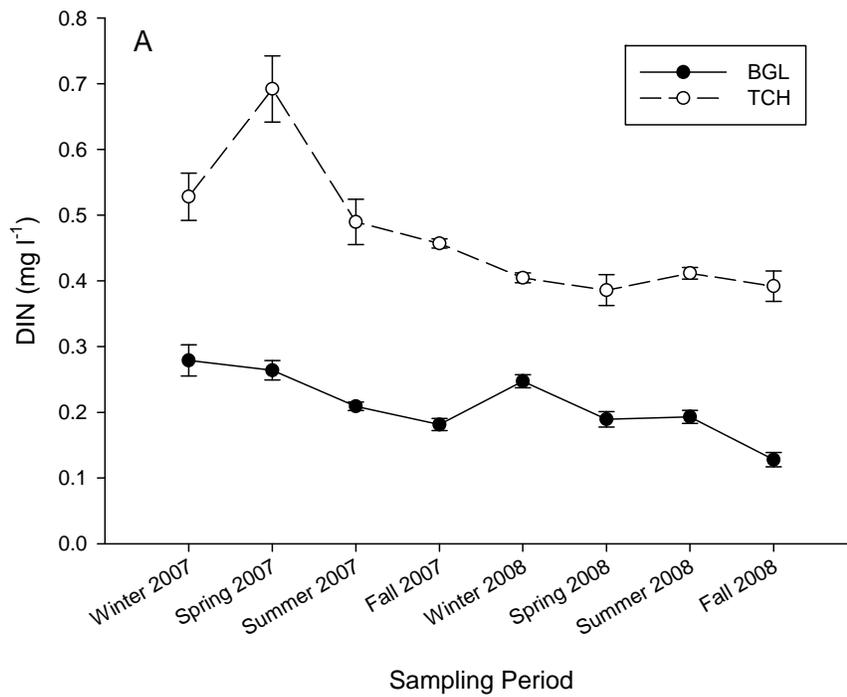


Fig. 3 Seasonal trends in ambient DIN (NO₃-N + NH₄-N) concentrations for (a) shaded and (b) unshaded sites in the four study streams in southeastern Louisiana.

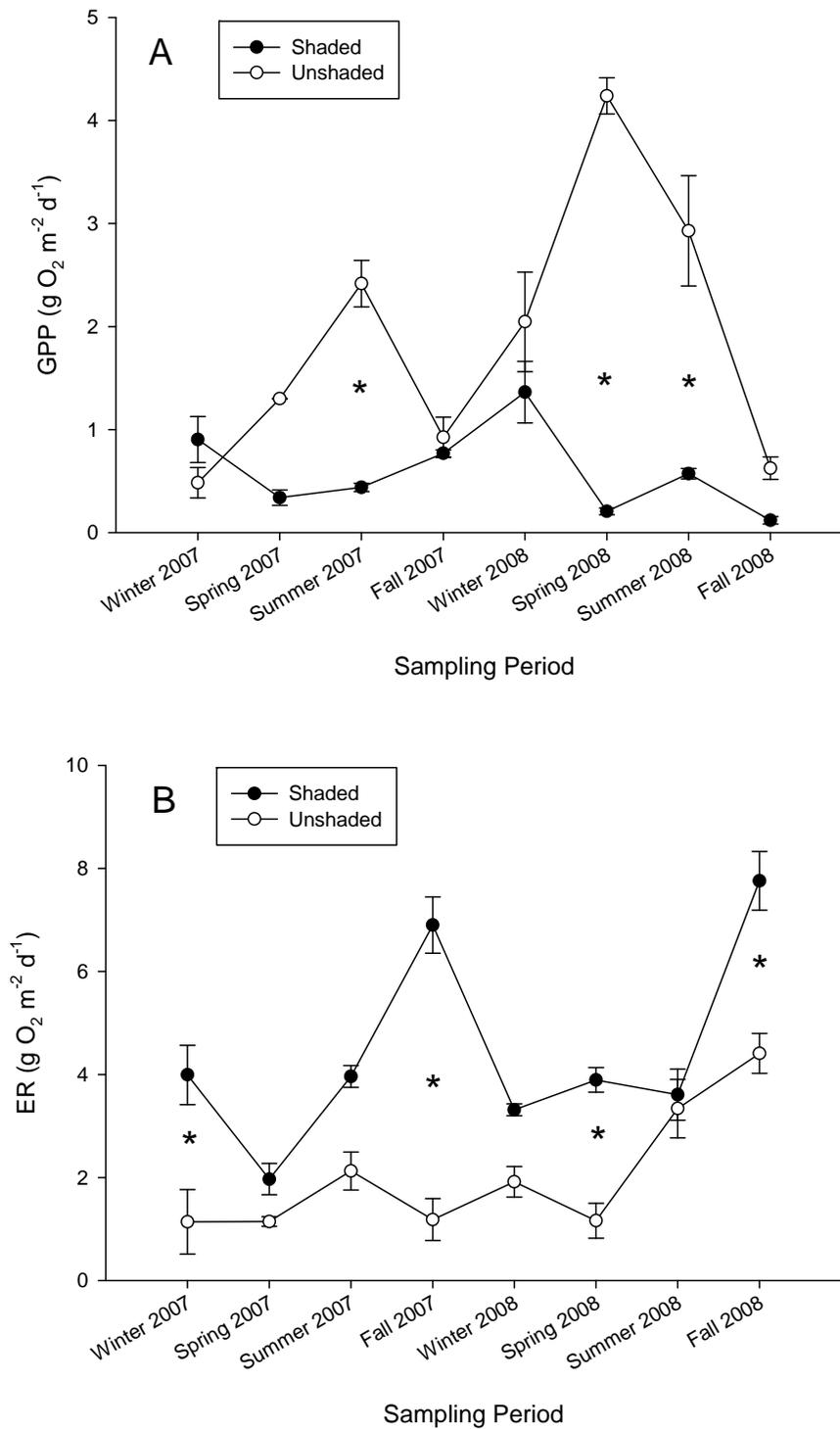


Fig. 4 Seasonal trends in (a) gross primary production (GPP) and (b) ecosystem respiration (ER) for shaded (●) and unshaded sites (○) in the four study streams in southeastern Louisiana. Tukey's pairwise significant differences at $p < 0.05$ are marked by *.

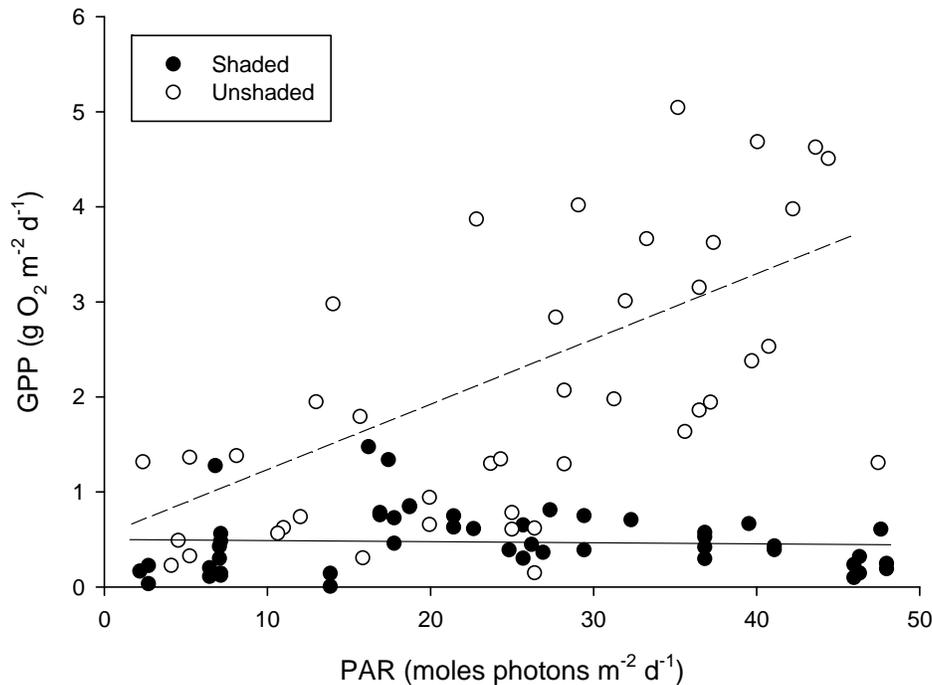


Fig. 5 The relationship between daily gross primary production (GPP) and daily photosynthetically active radiation (PAR) in shaded (closed circles; $R^2 > 0.01$, $p = 0.68$; $n = 48$) and unshaded (open circles; $R^2 = 0.39$, $p < 0.01$, $n = 42$) study streams in southeastern Louisiana.

rates in shaded streams occurred in fall and winter under moderate PAR readings. Spring 2008 had the highest average levels of PAR but registered some of the lowest GPP rates during the study, whereas spring 2007 had some of the lowest readings in both PAR and GPP. A comparison of GPP versus PAR slopes were significantly different (ANCOVA; $p < 0.01$; see Appendix Table A2.3).

Shaded streams were characterized by greater abundance of LWD (Fig. 6; Appendix Table A2.4) and percent BOM (Fig. 7) than unshaded streams. Not only were densities of LWD lower at the unshaded sites, but elevated discharges associated with passing storms continually flushed instream LWD downstream to a greater extent than in the shaded systems (JLW,

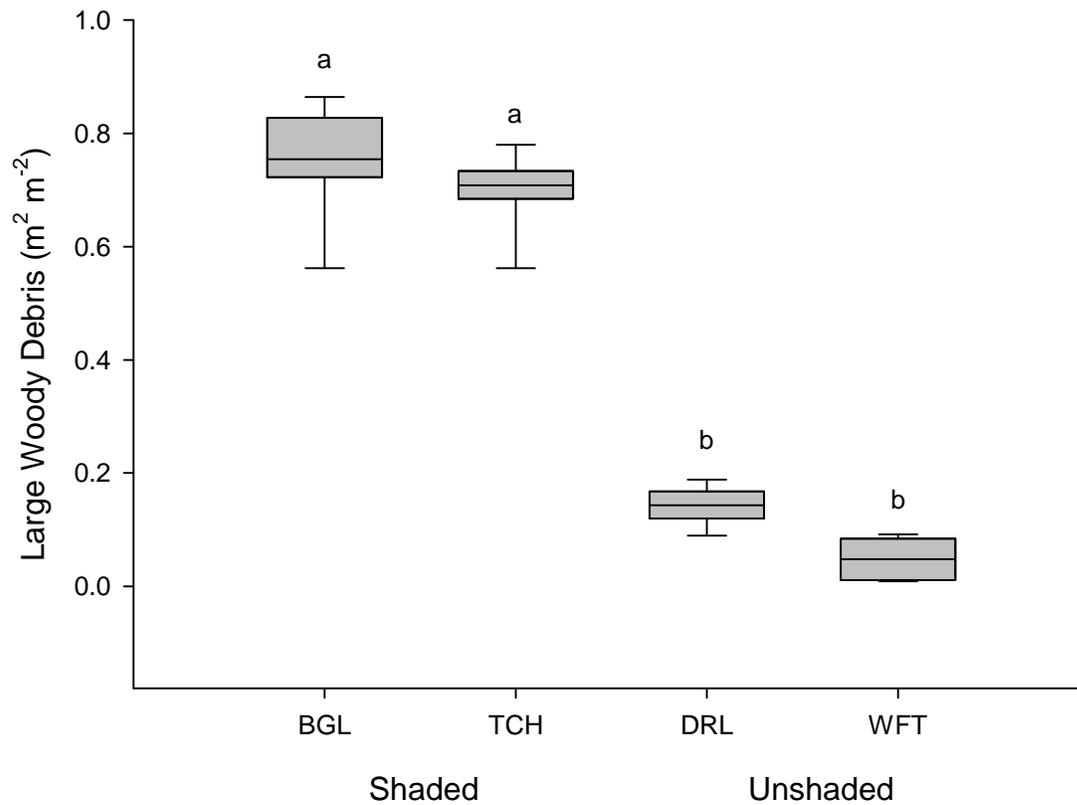


Fig. 6 Differences in LWD abundance in shaded and unshaded streams in southeastern Louisiana. BGL and TCH are significantly higher ($p < 0.01$) from DRL and WFT based on Tukey's post-hoc test (ANOVA: $p < 0.01$, $n = 30$, $F = 236.87$).

personal observation). Percent BOM peaked after fall leaf senescence at both shaded and unshaded sites, and then decreased over the year as this organic material was processed. The highest BOM values recorded during the study occurred in fall 2008, coincident with high densities of leaf litter on the stream bottom at BGL, TCH, and WFT. Only site and season were significantly related to BOM in the streams, with BGL and DRL consistently having the highest and lowest BOM levels, respectively (i.e., no significant interactions; Appendix Table A2.5).

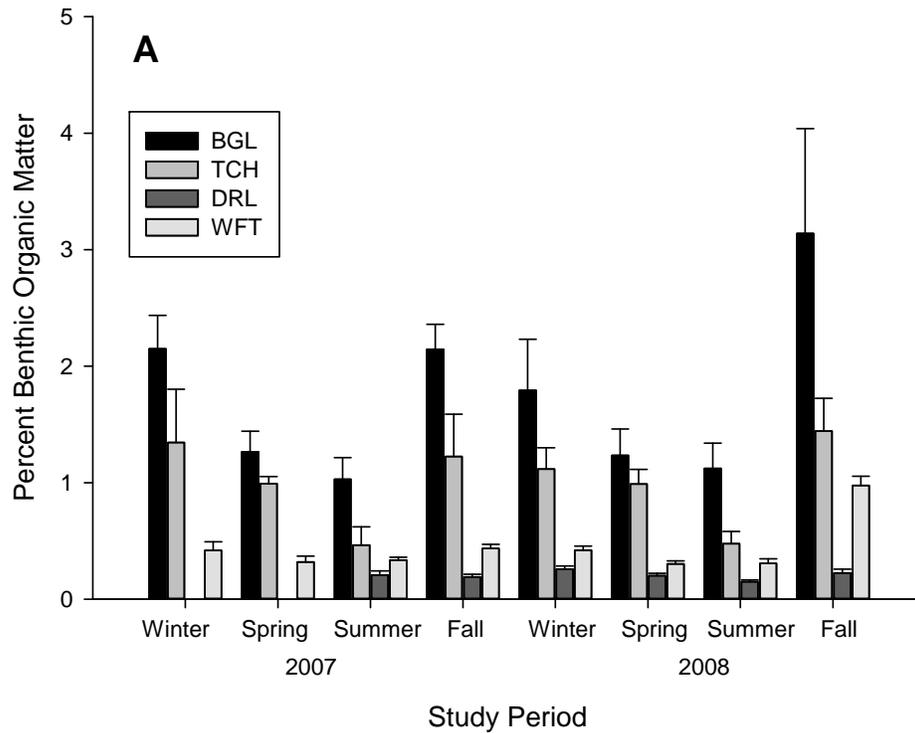


Fig. 7 Seasonal levels of BOM in shaded (BGL and TCH) and unshaded streams (DRL and WFT) in southeastern Louisiana.

Discussion

These findings underscore the importance of both predictable and stochastic factors in determining stream metabolism in low gradient, sand dominated coastal plain streams.

Temporally, GPP typically varies predictably throughout the day from sunrise to sunset and seasonally with changes in temperature (Wiley et al., 1990) and the duration and angle of incident sunlight (Young et al., 2008). Leaf abscission in fall results in increased light levels and GPP in forested streams—although leaf cover on the surface of the stream may limit light temporarily, but also increases OM inputs that drive heterotrophic processes and elevate ER.

Stochastically, GPP can vary throughout the day with changes in cloud cover, as well as storm-

related increases in stream discharge, with higher flow velocities depressing GPP through higher turbidity and algal scouring (Uehlinger and Naegeli, 1998; Uehlinger, 2000), while concurrently elevating ER through increased allochthonous inputs of OM from the surrounding riparian zone (Roberts et al., 2007) and re-suspension of buried OM (Metzler and Smock, 1990). On longer time scales, interannual hydrologic variability may be manifested through changes to metabolism rates downstream along the river continuum (Young and Huryn, 1996). Although annual and seasonal trends suggested some predictability in stream metabolism is possible for my study streams, significant interactions for both GPP and ER throughout the study highlight the importance of stochastic variation in determining rates of GPP and ER.

Although all of the study streams were low-gradient systems characteristic of coastal plain ecoregions in the southeastern U.S., structural and functional differences among streams were evident. The lower pH values observed in the two shaded streams were likely related to either higher levels of dissolved organic acids (e.g., fulvic or humic acids) in the water provided by the greater supply of woody debris and BOM (Petrin et al., 2008) or were a product of ER as dissolved carbon dioxide combined with water to form carbonic acid (Wetzel and Likens, 1991). Incident sunlight was much higher in unshaded systems, which typically resulted in higher mean spring and summer temperatures relative to the two shaded streams. Seasonal variation in water velocity, discharge, and depth among streams was due to differences in precipitation among catchments, although BGL tended to have consistently lower water velocities due to several debris dams in the study reach. I concluded that there was an undetectable input of groundwater into these streams based on the conservation of NaCl between upstream and downstream stations during slug injections, and thus did not correct GPP and ER estimates for groundwater inputs (Gordon et al., 2004; Bott, 2006).

Ambient stream PO₄-P concentrations tended to vary asynchronously with GPP, particularly in BGL and TCH. This pattern is consistent with previous reports of increased spring and summer nutrient concentrations in shaded streams that are tied to canopy closure and decreased PAR and algal biomass (Hill et al., 2001; Roberts et al., 2007). In BGL, TCH, and WFT, peaks in GPP each year were typically associated with relatively low levels of PO₄-P, likely due to uptake by algae or differences in supply. This inverse relationship contrasts with results presented by Mulholland et al. (2001), who reported in a geographically-broad study of stream metabolism that PO₄-P was positively correlated with both stream GPP and ER. This contradiction may be due to several factors, including differences in PO₄-P limitation among streams, as well as the duration of stream metabolism studies. The lowest ambient PO₄-P concentrations in my study streams were nearly an order of magnitude higher than the highest value reported in Mulholland et al. (2001), suggesting that this nutrient may not be limiting in these systems. In addition, PO₄-P concentrations varied substantially among seasons and years, and results of my study may not correlate with other assessments conducted over short periods of time during summer (e.g., Bott et al., 1985; Mulholland et al., 2001; Bernot et al., 2010).

Concentrations of DIN in the study streams were dominated by NH₄-N rather than NO₃-N, which is not common in most temperate streams, but is not unusual in streams of the Gulf and Atlantic coasts (Stanley and Ward, 1997; Clark et al., 2000 and appendices; NCASI, 2001), particularly in Louisiana coastal plain streams (D.G. Kelly, LSU AgCenter, unpublished data). Sources of NH₄-N can include upwelling from the hyporheic zone or groundwater input (Hill et al., 1998), depletion of oxygen and mineralization of organic N during decomposition of OM (Stanley and Ward, 1997), export from riparian forests associated with storms (Hill, 1993), and possibly from secondary wastewater effluent. Depositional streams usually have substantial

exchange of water with their hyporheic zones, which is the most likely source of $\text{NH}_4\text{-N}$ in these streams (Metzler and Smock, 1990). Chronic hypoxia could possibly contribute significantly to high $\text{NH}_4\text{-N}$ concentrations in many stagnant, organically rich Louisiana streams, but these conditions were not evident in this study. It has been suggested that some stream reaches may function as a source of $\text{NH}_4\text{-N}$ through excretion by grazers or regeneration by algal production (Roberts and Mulholland, 2007), which could have also contributed to the observed dominance of $\text{NH}_4\text{-N}$ in these systems; however, grazer densities have yet to be assessed in the study streams

Between the two shaded streams, TCH had consistently higher concentrations of both $\text{PO}_4\text{-P}$ and TIN than BGL throughout the study. Similarly, although TIN concentrations were similar between the two open streams, WFT often exhibited higher $\text{PO}_4\text{-P}$ concentrations than DRL. However, these differences were not reflected in consistently higher or lower GPP or ER rates between TCH and BGL, or between WFT and DRL. My *a priori* division of streams into high and low nutrient streams was not warranted, as apparently both nitrogen and phosphorus are adequate algal growth (Larned, 2010) or affecting heterotrophic activity. Based on the coarse guidelines for nutrient criteria suggested by Dodds et al. (1998), each of these streams was near or above the oligotrophic-mesotrophic boundary for both nitrogen and phosphorus as simple inorganic forms, and there is probably a surplus of nutrients in these systems.

In contrast to nutrients, which were often at similar levels in all four streams, there were clear differences in patterns of GPP between shaded and unshaded streams throughout the study period. In shaded streams, ranges of annual GPP rates were similar to those in other forested systems (Mulholland et al., 2001; Izagirre et al. 2008; Bernot et al., 2010), with the highest rates occurring early in the year when the canopy was open. Additional measurements of GPP and

canopy cover during leaf emergence in 2008 and 2009 indicated that as leaf density increased, GPP dropped precipitously (Fig. 8), likely due to interception of PAR by the developing canopy (Hill et al., 2001; Roberts et al., 2007). Low spring GPP rates in these systems during this time may have also been due to lags in algal population shifts from shade-intolerant to shade-tolerant species (Hill, 1996). This pattern of increased GPP in dense-canopy systems prior to leaf-out was apparently unrelated to substrate composition, having also been reported for a sand-gravel stream in northeastern Spain (Acuña et al., 2004) and a bedrock-cobble stream in eastern Tennessee (Roberts et al., 2007).

In unshaded streams, the temporal pattern of higher GPP rates in spring and summer was similar to other unshaded stream systems (Uehlinger and Naegeli, 1998; Uehlinger, 2000; Izagirre et al., 2008), and light availability was likely an important factor as high PAR was associated with higher GPP rates in these streams. It is unlikely that nutrients limited GPP, and with low canopy cover and relatively clear water, GPP rates are likely limited by hour-to-hour variation in cloud cover, angle of incident light, or hours of daylight, with the latter two a function of season. Importantly, the sediment of these streams is comprised mostly of sand, which is easily moved during high discharge events associated with storms (Metzler and Smock, 1990), and sediment stability is probably also a significant factor affecting GPP through algal scouring (e.g. Peterson, 1996; Atkinson et al., 2008).

In the two shaded streams, ER tracked the seasonal pattern of benthic OM content, with higher rates in the fall corresponding to leaf abscission and the input of leaf litter. The higher benthic OM and LWD abundance in the shaded systems seemed to allow for consistently higher levels of carbon to fuel greater ER rates over the course of the year relative to the open streams,

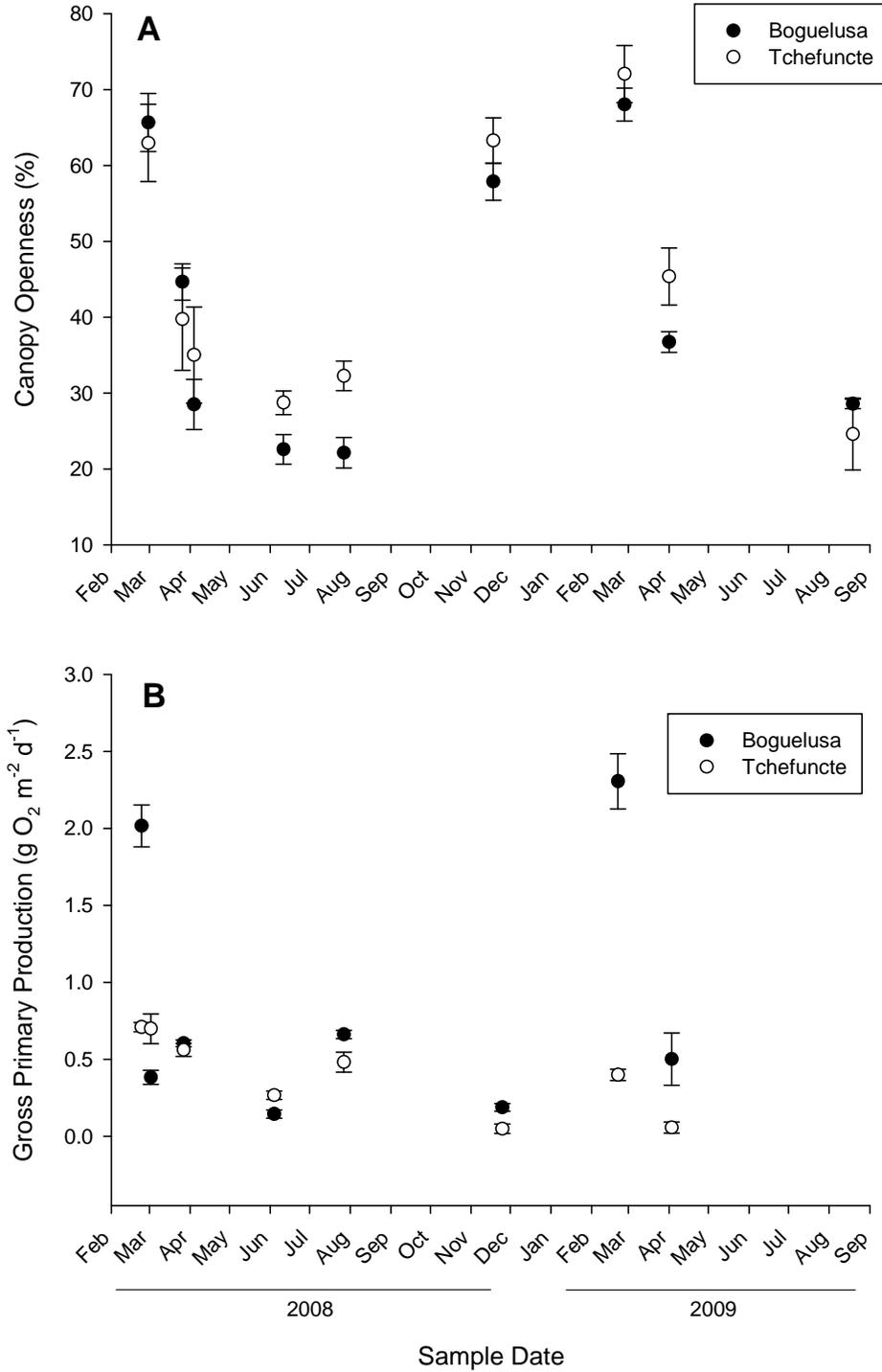


Fig. 8 Gross primary production through time in the two shaded study streams in southeastern Louisiana. Extra measurements from 2008 and 2009 supplement previously reported data.

although ER rates in both systems were similar to those found in previous studies (Mulholland et al., 2001; Bott et al., 2006; Bernot et al. 2010). In the unshaded streams, LWD and leaf litter were usually washed downstream or buried by sedimentation after spates, which likely depressed ER (Acuña et al., 2004; Houser et al., 2005). Buried OM is processed much more slowly in the hyporheic zone in sandy streams (Metzler and Smock, 1990) and may not contribute significantly to ER, regardless of the extent of the hyporheic zone in these types of systems. Interestingly, I observed strikingly different leaf litter abundance in WFT between fall 2007 (minimal abundance) and fall 2008 (prevalent leaf packs, with leaf litter covering a good percentage of the stream bottom). These differences were reflected in an almost 20-fold increase in ER between the two years, emphasizing the potentially important role of stochastic differences in OM inputs in determining stream ER rates. Summer peaks in ER were exhibited in the unshaded streams at both WFT (2007) and DRL (2008) and may have been driven by algal respiration, autotrophic OM production, or temperature (Wiley et al., 1990; Young and Huryn, 1999; McTammany et al., 2007) in addition to storm-related changes in benthic OM levels.

Net ecosystem production (NEP) is the difference between GPP and ER and describes the relative importance of autochthonous and allochthonous energy sources in a stream (Young et al., 2008). Streams that rely on upstream or outside sources of OM to support primary consumers are considered net heterotrophic ($ER > GPP$), whereas systems that depend on internal energy derived from photosynthesis are considered net autotrophic. The shaded streams remained mostly net heterotrophic throughout the study period, suggesting that allochthonous sources of OM such as riparian LWD and leaf litter fueled the energy flow in these 2nd order streams. In contrast, allochthonous OM was much less abundant in the unshaded streams, but increased levels of incident light allowed these systems to become periodically net autotrophic

especially in summer. These results were similar to the findings of Hill and Harvey (1980), who reported that periphyton had increased activity in unshaded study sites compared with shaded sites.

Light saturation or inhibition of algal production was not evident in either the shaded or unshaded systems. Canopy closure in the shaded streams likely controlled GPP during peak sunlight hours in spring and summer, and there was little correlation between PAR and GPP when the canopy was open in fall and winter. In the unshaded streams, I observed a linear relationship between PAR and GPP, and I believe that substrate stability is a much more important factor limiting algal growth and GPP than light availability in these streams (e.g., Atkinson et al., 2008). The magnitude of herbivory or chemo-inhibition by various organic or inorganic pollutants was not assessed (see review by Young et al., 2008).

One of the largest sources of error in calculating GPP and ER with an open-system method is estimating reaeration. Reaeration rates can be assessed with direct measurement via tracer gas injections, nocturnal and diurnal regressions of the change in oxygen concentration versus oxygen saturation, and empirical equations, all of which have advantages and disadvantages. Reaeration values calculated using the EDM for the study streams were within the range of k_{O_2} values estimated from diurnal regression (Atkinson et al., 2008) and measured with propane evasion (Houser et al., 2005) in sandy streams. Mulholland et al. (2001) reported that EDM usually underestimated k_{O_2} values measured via gas evasion, especially in shallow streams (< 12 cm) and turbulent systems. Because my study streams were not turbulent, had low velocities with seemingly laminar flow, and typically averaged over 20 cm in depth, I believe my estimated reaeration values using the EDM were an acceptable substitute for gas tracer and nocturnal regression methods (Aristegi et al., 2009).

I agree with Young et al. (2008) that measurements of functional attributes such as stream metabolism are an important complement to physicochemistry and biotic community composition for assessment of lotic system health. However, seasonal and stochastic variation in metabolism components must be taken into consideration when using functional characteristics as assessment metrics for determining stream impairment. Attempts to apply regional patterns or general predictions of stream metabolism rates to specific streams have only had moderate success (Wiley et al., 1990; Young and Huryn, 1999; Mulholland et al., 2001; Izagirre et al., 2008; Bernot et al., 2010). For example, local geologic or geographic characteristics such as high valley walls (Young and Huryn, 1999) or small riparian canopies in arid systems (Mulholland et al., 2001) can either limit or stimulate GPP, yet are not indicative of unhealthy streams. Izagirre et al. (2008) reported GPP rates in streams categorized as oligotrophic that far exceeded rates recognized as “poor” ($>7 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$), or indicative of degraded stream conditions (Young et al. 2008), as well as mean GPP rates of $\sim 5 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$, which would be considered “satisfactory” ($3.6 - 7 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$; Young et al. 2008), for streams categorized as polluted (Izagirre et al., 2008). In streams characterized by constantly moving sand substrates, GPP rates are typically low but are considered “healthy” ($0.5 - 3.5 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$) on the Young et al. (2008) scale (Atkinson et al., 2008). Rates of both GPP and ER in my study streams indicated either “healthy” or “satisfactory” conditions. Although the relatively high concentrations of phosphorus and nitrogen could suggest water quality problems, all of these streams appear to have diverse invertebrate and fish populations (unpublished data). I agree with Izagirre et al. (2008) that there is a lack of reliable metabolism data for reference streams, as well as from streams with significant seasonal and/or stochastic fluctuations in GPP and ER, such as those found along the sand-dominated coastal plain. Metabolism varies substantially in these streams

through time, and is most closely tied to canopy density (shaded streams) and substrate instability (open streams). Overall patterns of ER in the study streams appeared to be controlled by the OM inventory of the stream, as annual leaf fall boosted ER rates in both shaded and unshaded streams. Assessment of seasonal and stochastic variation would be of particular importance if these metrics were used to evaluate ecosystem health in coastal plain streams along the Gulf of Mexico.

Lastly, streams in Louisiana have been rarely studied (but see Kaller and Kelso, 2006a, b, c; Kaller and Kelso, 2007) and represent a rich opportunity for research. These streams are not typical of the type of streams consistently reported stream research literature. For example, the prevalence of high concentrations of $\text{NH}_4\text{-N}$ has only been found in a few other streams and could be a fruitful area for future study and assessment. I have shown that the use of PAR recorded from areas away from the stream can also be misleading as previous studies have shown that after leaf growth in the riparian canopy occurs, the amount of light that actually reaches the streams drops precipitously (e.g., Hill et al. 2001; Roberts et al., 2007). Other areas of future research for these streams include invertebrate and grazer assessment, OM budget analyses including the partitioning of labile to refractory fractions, and nutrient uptake and/or processing studies.

References

- Acuña, V., A. Giorgi, I. Munoz, U. Uehlinger, and S. Sabater, 2004. Flow extremes and benthic organic matter shape the metabolism of a headwater Mediterranean stream. *Freshwater Biology* 49:960-971.
- APHA (American Public Health Association), 2005. Standard methods for the examination of water and wastewater, 21st edition. American Public Health Association. Washington, DC.

- Aristegi, L., O. Izagirre, and A. Elozegi, 2009. Comparison of several methods to calculate reaeration in streams, and their effects on estimation of metabolism. *Hydrobiologia* 635:113-124.
- Atkinson, B.L., M.R. Grace, B.T. Hart, and K.E.N. Vanderkruk, 2008. Sediment instability affects the rate and location of primary production and respiration in a sand-bed stream. *Journal of the North American Benthological Society* 27:581-592.
- Bernot, M.J., D.J. Sobota, R.O. Hall, P.J. Mulholland, W.K. Dodds, J.R. Webster, J.L. Tank, L.R. Ashkenas, L.W. Cooper, C.N. Dahm, S. Findlay, S.V. Gregory, N.B. Grimm, S.K. Hamilton, S.L. Johnson, W.H. McDowell, J.L. Meyer, B.J. Peterson, G.C. Poole, H. M. Valett, C. Arango, J.J. Beaulieu, A.J. Burgin, C. Crenshaw, A.M. Helton, L. Johnson, J. Merriam, B.R. Niederlehner, J.M. O'Brien, J.D. Potter, R.W. Sheibley, S.M. Thomas, and K. Wilson, 2010. Inter-regional comparison of land-use effects on stream metabolism. *Freshwater Biology* 55:1874-1890.
- Bott, T.L., J.T. Brock, C.S. Dunn, R.F. Naiman, R.W. Ovink, and R.C. Petersen, 1985. Benthic community metabolism in four temperate stream systems: an inter-biome comparison and evaluation of the river continuum concept. *Hydrobiologia* 123:3-45.
- Bott, T.L., 2006. Primary production and community respiration. In: Hauer, F.R., and G.A. Lamberti, (editors), *Methods in Stream Ecology*, 2nd edition. Academic Press, Burlington, MA: 663-690.
- Bott, T.L., D.S. Montgomery, J.D. Newbold, D.B. Arscott, C.L. Dow, A.K. Aufdenkampe, J.K. Jackson, and L.A. Kaplan, 2006. Ecosystem metabolism in stream of the Catskill Mountains (Delaware and Hudson River watersheds) and Lower Hudson Valley. *Journal of the North American Benthological Society* 25:1018-1044.
- Clark, G.M., D.K. Mueller, and M.A. Mast, 2000. Nutrient concentrations and yields in undeveloped stream basins of the United States. *Journal of the American Water Resources Association* 36:849-860.
- Dodds, W.K., J.R. Jones, and E.B. Welch, 1998. Suggested classifications of stream trophic state: distributions of temperate stream types by chlorophyll, total nitrogen, and phosphorus. *Water Research* 32:1455-1462.
- Elmore, H.L., and W.F. West, 1961. Effect of water temperature on stream reaeration. *Journal of the Sanitary Engineering Division ASCE* 87:59-71.
- Felley, J.D., 1992. Medium-low-gradient streams of the Gulf Coastal Plain. In: Hackney, C.T., S.M. Adams, and W.H. Martin (editors). *Biodiversity of the Southeastern United States: Aquatic Communities*. John Wiley and Sons, New York: 233-269.

- Fellows, C.S., J.E. Clapcott, J.W. Udy, S.E. Bunn, B.D. Harch, M.J. Smith, and P.M. Davies, 2006. Benthic metabolism as an indicator of stream ecosystem health. *Hydrobiologia* 572:71-87.
- Frazer, G.W., C.D. Canham, and K.P. Lertzman, 1999. Gap Light Analyzer (GLA): Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation. Simon Fraser, British Columbia: 36 pp.
- Gerull, L., A. Frossard, M.O. Gessner, and M. Mutz, 2012. Effects of shallow and deep sediment disturbance on whole-stream metabolism in experiment sand-bed flumes. *Hydrobiologia* 683:297-310.
- Gordon, N.D., T.A. McMahon, B.L. Finlayson, G.J. Gippel, and R.J. Nathan, 2004. Stream Hydrology: An Introduction for Ecologists, 2nd edition. Wiley, England: 429 pp.
- Hill, A.R., 1993. Nitrogen dynamics of storm runoff in the riparian zone of a forested watershed. *Biogeochemistry* 20:19-44.
- Hill, A.R., C.F. Labadia, and K. Sanmugadas, 1998. Hyporheic zone hydrology and nitrogen dynamics in relation to the streambed topography of N-rich stream. *Biogeochemistry* 42:285-310.
- Hill, W.R., and B.C. Harvey, 1980. Periphyton responses to higher trophic levels and light in a shaded stream. *Canadian Journal of Fisheries and Aquatic Sciences* 47:2307-2314.
- Hill, W.R., 1996. Effects of light. In: Stevenson, R.J., M.L. Bothwell, and R.L. Lowe, (editors), *Algal Ecology: Freshwater Benthic Ecosystems*. Academic Press, Burlington, MA: 121-149.
- Hill, W.R., P.J. Mulholland, and E.R. Marzolf, 2001. Stream ecosystem responses to forest leaf emergence in spring. *Ecology* 82:2306-2319.
- Hornberger, G.M., and M.G. Kelly, 1975. Atmospheric reaeration in a river using productivity analysis. *Journal of the Environmental Engineering Division-ASCE* 101:729-739.
- Houser, J.N., P.J. Mulholland, and K.O. Maloney, 2005. Catchment disturbance and stream metabolism: patterns in ecosystem respiration and gross primary production along a gradient of upland soil and vegetation disturbance. *Journal of the North American Benthological Society* 24:538-552.
- Izagirre, O., U. Agirre, M. Bermejo, J. Pozo, and A. Elosegi, 2008. Environmental controls of whole-stream metabolism identified from continuous monitoring of Basque streams. *Journal of the North American Benthological Society* 27:252-268.

- Kaller, M.D., and W.E. Kelso, 2006a. Occurrence of freshwater bivalves in a chronically hypoxic coastal stream in Louisiana, USA. *Journal of Freshwater Ecology* 21:355-357.
- Kaller, M.D., and W.E. Kelso, 2006b. Swine activity alters invertebrate and microbial communities in a coastal plain watershed. *American Midland Naturalist* 156:163-177.
- Kaller, M.D., and W.E. Kelso, 2006c. Short-term decompositional state does not influence use of wood by macroinvertebrates in subtropical, coastal plain streams. *Hydrobiologia* 571:157-167.
- Kaller, M.D., and W.E. Kelso, 2007. Association of macroinvertebrate assemblages with dissolved oxygen concentration and wood surface area in selected subtropical streams of the southeastern USA. *Aquatic Ecology* 41:95-110.
- Kroening, S.E., 2004. Streamflow and Water-Quality Characteristics at Selected Sites of the St. Johns River in Central Florida, 1933 to 2002: U.S. Geological Survey Scientific Investigations Report 2004-5177, 102 p.
- Lewis, T., and L.R. Taylor, 1967. *Introduction to Experimental Ecology*. Academic Press, London: 401 pp.
- Larned, S.T., 2010. A prospectus for periphyton: recent and future ecological research. *Journal of the North American Benthological Society* 29:182-206.
- Marzolf, E.R., P.J. Mulholland, and A.D. Steinman, 1994. Improvements to the diurnal upstream-downstream dissolved oxygen change technique for determining whole-stream metabolism in small streams. *Canadian Journal of Fisheries and Aquatic Sciences* 51:1591-1599.
- McCree, K.J., 1972. Test of current definitions of photosynthetically active radiation against leaf photosynthesis data. *Agricultural Meteorology* 10:443-453.
- McTammany, M.E., J.R. Webster, E.F. Benfield, and M.A. Neatrour, 2003. Longitudinal patterns of metabolism in a southern Appalachian river. *Journal of the North American Benthological Society* 22:359-370.
- Meyer, J.L., and R.T. Edwards, 1990. Ecosystem metabolism and turnover of organic carbon along a blackwater river continuum. *Ecology* 71:668-677.
- Metzler, G.M., and L.A. Smock, 1990. Storage and dynamics of subsurface detritus in a sand-bottomed stream. *Canadian Journal of Fisheries and Aquatic Sciences* 47:588-594.
- Mulholland, P.J., C.S. Fellows, J.L. Tank, N.B. Grimm, J.R. Webster, S.K. Hamilton, E. Marti, L. Ashkenas, W.B. Bowden, W.K. Dodds, W.H. McDowell, M.J. Paul, and B.J. Peterson, 2001. Inter-biome comparison of factors controlling stream metabolism. *Freshwater Biology* 46:1503-1517.

- National Council for Air and Stream Improvement, Inc. (NCASI), 2001. Patterns and processes of variation in nitrogen and phosphorus concentrations in forested streams. Technical Bulletin No. 836. Research Triangle Park, NC: National Council for Air and Stream Improvement, Inc.
- Peterson, C.G., 1996. Response of benthic algal communities to natural physical disturbance. In: Stevenson, R.J., M.L. Bothwell, and R.L. Lowe, (editors), *Algal Ecology: Freshwater Benthic Ecosystems*. Academic Press, Burlington, MA: 375-402.
- Petrin, Z., G. England, and B. Malmqvist, 2008. Contrasting effects of anthropogenic and natural acidity in streams: a meta-analysis. *Proceedings of the Royal Society B* 275:1143-1148.
- Roberts, B.J., P.J. Mulholland, and W.R. Hill, 2007. Multiple scales of temporal variability in ecosystem metabolism rates: results from 2 years of continuous monitoring in a forested headwater stream. *Ecosystems* 10:588-606.
- Roberts, B.J., and P.J. Mulholland, 2007. In-stream biotic control on nutrient biogeochemistry in a forested stream, West Fork of Walker Branch. *Journal of Geophysical Research* 112:G04002, doi:04010.01029/02007JG000422.
- Rosemond, A.D., P.J. Mulholland, and J.W. Elwood, 1993. Top-down and bottom-up control of stream periphyton: effects of nutrients and herbivores. *Ecology* 74:1264-1280.
- Rosemond, A.D., 1994. Multiple factors limit seasonal variation in periphyton in a forest stream. *Journal of the North American Benthological Society* 13:333-344.
- SAS Institute Inc., 2011. *SAS/STAT® 9.3 User's Guide*. Cary, NC: SAS Institute Inc.
- Stanley, E.H., and A.K. Ward, 1997. Inorganic nitrogen regimes in an Alabama wetland. *Journal of the North American Benthological Society* 16:820-832.
- Tsivoglou, E.C., and L.A. Neal, 1976. Tracer measurement of reaeration: III. predicting the reaeration capacity of inland streams. *Journal of the Water Pollution Control Federation* 48:2669-2689.
- Uehlinger, U., and M.W. Naegeli, 1998. Ecosystem metabolism, disturbance, and stability in a prealpine gravel bed river. *Journal of the North American Benthological Society* 17:165-178.
- Uehlinger, U., 2000. Resistance and resilience of ecosystem metabolism in a flood-prone river system. *Freshwater Biology* 45:319-332.
- Valett, H.M., S.G. Fisher, N.B. Grimm, and P. Camill, 1994. Vertical hydrologic exchange and ecological stability of a desert stream ecosystem. *Ecology* 75:548-560.

- Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell, and C.E. Cushing, 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37:130-137.
- Wallace, J.B., and A.C. Benke, 1984. Quantification of wood habitat in subtropical coastal plain streams. *Canadian Journal of Fisheries and Aquatic Sciences* 41:1643-1652.
- Wetzel, R.E., and G.E. Likens, 1991. *Limnological Analyses*. Springer-Verlag, New York: 391 pp.
- Wiley, M.J., L.L. Osborne, and R.W. Larimore, 1990. Longitudinal structure of an agricultural prairie river system and its relationship to current stream ecosystem theory. *Canadian Journal of Fisheries and Aquatic Sciences* 47:373-384.
- Young, R.G., and A.D. Huryn, 1996. Interannual variation in discharge controls ecosystem metabolism along a grassland river continuum. *Canadian Journal of Fisheries and Aquatic Sciences* 53:2199-2211.
- Young, R.G., and A.D. Huryn, 1999. Effects of land use on stream metabolism and organic matter turnover. *Ecological Applications* 9:1359-1376.
- Young, R.G., C.D. Matthaei, and C.R. Townsend, 2008. Organic matter breakdown and ecosystem metabolism: functional indicators for assessing river ecosystem health. *Journal of the North American Benthological Society* 27:605-625.

CHAPTER 3. MULTIVARIATE ANALYSES OF ECOSYSTEM METABOLISM IN COASTAL PLAIN STREAMS IN SOUTHEAST LOUISIANA: EFFECTS OF STREAM SIZE AND LAND USE PATTERNS

Introduction

Streams are strongly connected to the landscape in which they flow and any activity that takes place in the watershed is ultimately reflected in the structure and function of the stream (Hynes, 1975). Watershed activities that lead to changes in land use or anthropogenic disturbance that manifest as modifications to channel morphology or stream structure, increased sedimentation or nutrient concentrations, changes to biotic abundances or diversity, and/or alterations of ecological function (Allan, 2004). One ecological function that has become increasingly important is tracking the energy flow through lotic systems via stream metabolism studies and has received increased interest due to the potential role as a measurement of stream health (Tank et al., 2008; Young et al., 2008). Recently, several studies have attempted to ascertain the effects of land use changes or watershed disturbance on rates of ecosystem metabolism (e.g., Wiley et al., 1990; Young and Huryn, 1999; Houser et al., 2005; McTammany et al., 2007; Izagirre et al., 2008; Bernot et al., 2010; Hagen et al., 2010)

Measurement of stream ecosystem metabolism includes estimations of gross primary production (GPP), usually carried out by autotrophic organisms, and ecosystem respiration (ER), which includes both autotrophic and heterotrophic respiration. Odum (1956) originally used diel oxygen changes in the stream to calculate these two rates, and this method has been streamlined by recent modifications that have increased its accuracy and applicability (Marzolf et al., 1994; Marzolf et al., 1998; Young and Huryn, 1998). By comparing these rates, the dependence of the stream on outside sources of organic matter or instream productivity can be determined based on either net daily metabolism (NDM), which is the difference between GPP and ER, or the ratio of

GPP to ER, termed P/R (Bott, 2006). In general, a stream is considered net heterotrophic when NDM is negative or $P/R < 1$, and the biota in these streams is more dependent on outside sources of organic matter (OM). In contrast, streams are considered net autotrophic when NDM is positive or $P/R > 1$. In the latter situation, autotrophic processes dominate and a majority of OM accrual occurs via photosynthesis (Bott, 2006).

Ecosystem metabolism in lotic systems is generally related to system size in two ways. Lower rates of GPP occur in smaller systems due to light limitation by the riparian canopy, and as the stream widens, light limitation of autotrophs declines (Meyer and Webster, 1997; Young and Huryn, 1999). In smaller streams, the canopy provides abundant allochthonous OM input to heterotrophs to fuel respiration (Meyer and Webster, 1997), whereas in larger systems there is less direct allochthonous input and greater reliance on autochthonous production and delivery of fine particulate OM from upstream sources (Meyer and Edwards, 1990; McTammany et al., 2003; McTammany et al., 2007). Studies have shown that GPP usually increases in larger systems or along a downstream continuum and that ER can either remain constant or increase longitudinally, the former possibly driving the system towards autotrophy (Bott et al., 1985; Naiman et al., 1987; Minshall et al., 1992; McTammany et al., 2003). Geography can also have an effect on metabolism as autotrophy can exist in desert or grassland biomes in smaller streams due to a lack of canopy cover (Minshall, 1978; Wiley et al., 1990; Fisher et al., 1982; Mulholland et al., 2001). Metabolism studies across multiple stream sizes and biomes have yielded some patterns, but controls on metabolism rates at some locations are considered stream-specific (Bernot et al., 2010).

Several other factors have been shown to either enhance or limit rates of ecosystem metabolism in streams. Temperature often plays a fundamental role in regulating both rates of

primary production as well as respiration in streams (Bott et al., 1985; Sinsabaugh, 1997). In addition to the effects of light and temperature, GPP has also been shown to increase with as nutrient levels rise (Mulholland et al., 2001; Izagirre et al., 2008; Bernot et al., 2010; and Frankforter et al., 2010), but decrease with flooding (Uehlinger 2000, 2006; Roberts et al., 2007), herbivory (Rosemond et al., 1993; Ortiz-Zayas et al., 2005), turbidity (Young and Huryn, 1999; Hagen et al., 2010), and sediment instability (Biggs et al., 1999; Atkinson et al., 2008). In addition to increases in OM inputs such as woody debris or leaf litter from the canopy, ER rates have also been stimulated by increased interactions of the stream with its hyporheic zone (Grimm and Fisher, 1984; Fellows et al., 2001; Mulholland et al., 2001), increased nutrient levels (Mulholland et al., 2001; Hoellein et al., 2009; Bernot et al., 2010), and organic pollution (Bott et al., 2006; Izagirre et al., 2008). Disturbance by flooding has been shown to decrease ER by burying or removing OM from the stream (Metzler and Smock, 1990; Acuña et al., 2004), or stimulate ER by disturbing sediments and uncovering previously buried OM deposits (Metzler and Smock, 1990; Gerull et al., 2012) or providing carbon sources from the watershed (Roberts et al., 2007).

With increased interest in the use of ecosystem metabolism as a metric of stream health, the effects of stream size, spatial location, and land use changes within a watershed on GPP and ER rates must be established. Interbiome comparisons may be helpful in determining general continental patterns, but in order to recognize reference or environmentally-imperiled systems, more study sites within a region or within spatial proximity are necessary (e.g., McTammany et al., 2007; Izagirre et al., 2008; Hagen et al., 2010). The Louisiana Department of Environmental Quality has classified many streams in the state as impaired because of high fecal coliform counts, nutrient concentrations, and/or sediment loads, with all three having potential effects on

rates of ecosystem metabolism (see review by Young et al., 2008). I attempted to determine the spatial patterns and controls on rates of GPP and ER in Louisiana streams of various sizes with the predictions that (1) GPP rates will be lower in smaller streams and increase as streams become larger; (2) ER rates will dominate in smaller streams with higher canopy cover resulting in heterotrophic conditions; (3) as streams become larger, GPP rates will rise relative to ER rates resulting in increasing net autotrophy and NEP rates. Secondly, I wanted to determine the effect of nutrients and turbidity on GPP, and heterotrophic bacterial activity on ER. Lastly, I attempted to quantify the effects of land use changes on the possible controls of ecosystem metabolism.

Methods and Materials

In order to elucidate patterns and potential controls of stream GPP and ER along the Gulf coastal plain, I sampled 1st to 4th order streams in southeastern Louisiana during 2007 (17 streams) and 2008 (24 streams; Table 1; Fig. 1). Streams in this region are characterized by low-velocity laminar flows, relatively clear water, and mostly sandy substrates. Stream morphology ranges from incised channels with an intact forested canopy to shallow active channels that move laterally within a broad floodplain valley with little riparian canopy due to scouring of vegetation along the banks. All field sampling was performed over shortest possible time periods, July – August in 2007 and 2008, to minimize the effects of temporal environmental variation on stream metabolism.

At each study site, a 100-m reach was randomly placed at least 200 m upstream from an access point. At the bottom of the reach a YSI 6600EDS-S extended deployment water quality datasonde (YSI Incorporated; Yellow Springs, OH) was placed in a well-mixed portion of the stream to measure specific conductance, dissolved oxygen (DO), temperature, depth, pH, and

Table 1 Stream names and abbreviations used in this study along with Strahler stream order and watershed area (calculated in ArcMap 9.3) listed with increasing watershed area.

Stream Name	Code	Order	Watershed Area (Ha)
Dunn Creek	DNC	1	1177.78
Polly Creek	PLC	1	1451.48
Clear Creek	CLR	1	1587.17
Beaver Creek	BVR	2	2816.59
West Fork of Thompson Creek (Upper)	UWF	2	2897.62
Tchefuncte River	TCH	2	5109.96
Bogue Lusa	BGL	2	5210.40
Sandy Creek	SND	2	5369.87
Alexander Creek	ALX	2	6015.74
Bogue Falaya	BGF	2	6121.24
West Fork of Thompson Creek (Middle)	MWF	3	6903.01
Little Bayou Sara	LBS	3	8789.77
West Fork of Thompson Creek (Lower)	LWF	3	9231.13
Thompson Creek	TMP	2	10605.04
Silver Springs Creek	SSC	2	11516.92
Lawrence Creek	LAW	2	13164.15
Natalbany Creek	NTL	2	14306.75
Darling River	DAR	3	16874.19
Bayou Sara	BSA	4	17561.20
Comite River	CMR	3	20048.34
Tickfaw River	TCK	3	22799.67
Pushepatapa	PSH	3	33316.05
Tangipahoa River	TNG	3	62539.71
Amite River	AMT	4	145643.04

turbidity every 15 minutes for 3 consecutive days. DO was measured with Clark sensor and was calibrated in water-saturated air about 24 hours prior to deployment. Initial measurements of these water quality parameters plus %DO saturation were also taken with a YSI 6820 V2 multiparameter water quality unit prior to datasonde deployment and after retrieval to double-check calibration and to test for instrument drift. YSI 6820 datasondes were calibrated approximately weekly according to prescribed methods. Triplicate water samples were collected just upstream of each reach in well-rinsed 2-L polypropylene Nalgene bottles and stored at 4°C.

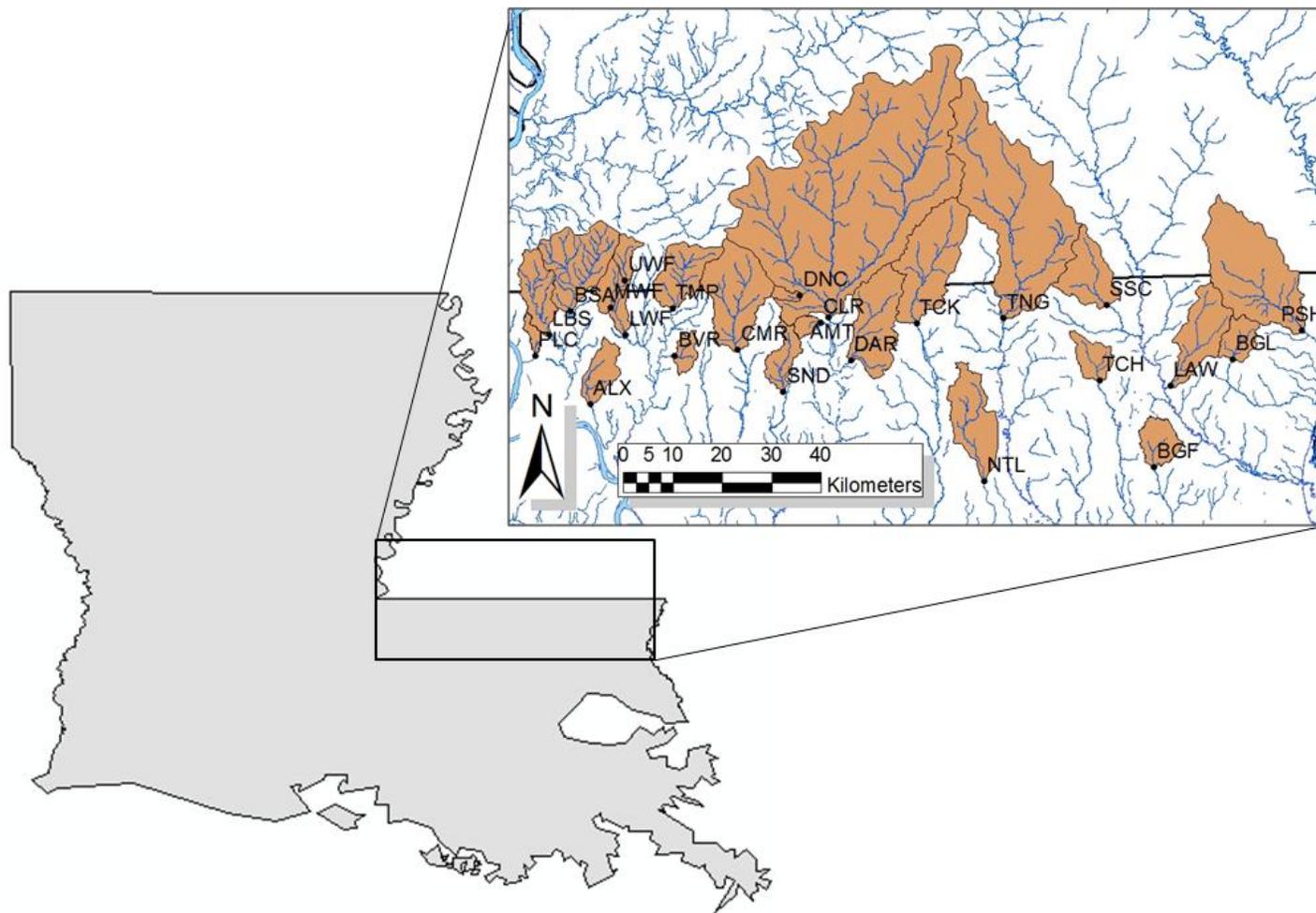


Fig. 1 Location of 24 watershed and streams reaches used in this study. Abbreviations correspond to Table 1.

One set of subsamples from these bottles was filtered through Whatman 0.45- μm glass microfiber filters and analyzed colorimetrically for nutrients ($\text{NO}_3\text{-N}$, $\text{NH}_4\text{-N}$, $\text{PO}_4\text{-P}$) with a Hach DR/2500 spectrophotometer according to methods prescribed by APHA (2005), while two other sets of subsamples were used to determine biochemical oxygen demand (BOD_{20}) and heterotrophic plate count (HPC) according to methods outlined in APHA (2005).

Ten evenly-spaced transects oriented perpendicular to the flow (~ 10 meters apart) were placed at each site. I recorded wetted width and depth (25%, 50%, and 75% across the stream, 30 measurements per reach), and visually estimated percent algal cover along a 50-cm band on each side of each transect (Gordon et al., 2004; Lewis and Taylor, 1967). Diameters of submersed wood that intersected the transect were measured to estimate surface area of large woody debris (LWD) per m^2 of stream bottom via the line-transect method (Wallace and Benke, 1984). In the middle of each transect approximately 1 m above the stream, a Kodak EasyShare Z740 camera fitted with an orthographic Opteka fish-eye lens was used to photograph the overlying canopy. The photograph was subsequently digitized in the laboratory, and canopy openness was determined with Gap Light Analyzer software v 2.0 (Frazer et al., 1999). I collected the upper 10 cm of sediment in a 320.5-cm^2 area with a PVC tube (inside diameter=10.1cm) at 5 randomly placed spots within the reach to determine benthic organic matter (BOM). Sediment samples were homogenized and subsampled, dried for at least 48 hours at 103°C , and then burned in a muffle furnace at 550°C for 4 hours. Subsequent weights were used to determine ash free dry mass (AFDM) and percent BOM content of sediment sampled throughout the reach.

Stream metabolism was calculated from diel DO curves as: $\Delta\text{DO} = \text{GPP} + \text{ER} + k(\text{C}_s - \text{C})$, where ΔDO is the daily change in dissolved oxygen, k is the reaeration coefficient, C is the

DO concentration, C_s is the DO concentration at saturation calculated from ambient stream temperature as prescribed by APHA (2005). The reaeration coefficient was calculated with the energy diffusion model (EDM): $k' \times \text{velocity} \times \text{slope}$, where k' changes with stream discharge (Bott, 2006). Channel gradient or slope (m m^{-1}) was taken from digital elevation models (see below). Velocity and discharge of the stream were measured via NaCl slug injection, where discharge (Q) is equal to the mass of Cl^- divided by the integral of the Cl^- concentration over background levels, and average water velocity is the time it takes for the peak Cl^- concentration to move through the reach (Gordon et al., 2004). Peaks in Cl^- concentration during the slug injections were measured by specific conductance with YSI 6820 V2 multiparameter water quality sonde (APHA, 2005). Net daily metabolism (NDM) was calculated as the sum of GPP and ER.

In 2009, I choose a subset of 13 streams to perform a concurrent propane-solute injection to measure gas reaeration in order to compare with EDM values. This subset included a range of conditions from small, shallow 1st order streams to deeper 3rd order streams. I injected a highly concentrated NaCl solution into the stream >50 m upstream of the reach at a constant volume through a tube that was split into 5 outlets to facilitate mixing across the width of the stream. Each of the outlets was calibrated by varying the tube sizes and/or adjustable clamps so all discharges were within ~10% of each other. Two multiparameter datasondes, calibrated in the same solution, were placed at the top and bottom of the reach to measure the change in conductivity every 15 seconds during the solute injection, and to calculate stream discharge and velocity for reaeration calculations via EDM (Stream Solute Workshop, 1990; Bott, 2006). During the solute injection, propane was bubbled through 5 cylindrical airstones (2.5 cm length x 1.3 cm diameter) placed longitudinally across the width of stream, again ensuring proper mixing.

About 30 minutes after steady state was reached during the solute injection, 5 replicate water samples were collected from the upstream and downstream stations in well-rinsed, 10-ml plastic syringes and 6 ml was injected into 10-ml pre-evacuated vacutainers. Vacutainers were air-equilibrated away from the stream, headspace gas was analyzed with a Shimadzu GC-2014 equipped with a Poropak 1/8-inch diameter, 6-foot length column (mesh 80/100) and a flame ionization detector at 150°C, and propane reaeration was calculated from the methods prescribed in Bott (2006). Propane reaeration was converted to oxygen with a factor of 1.39 (Rathbun et al., 1978).

Watersheds were delineated from digital elevation models (DEMs) created in ArcMap 9.3 (Environmental Systems Research Institute, Inc., Redlands, California) from Light Detection and Ranging (LIDAR) flights completed in 1999. Briefly, the location of the YSI 6600EDS-S datasonde was recorded with a Garmin GPSmap 60CS handheld GPS unit (Garmin International Inc., Olathe, KS) and superimposed over LIDAR cover layers in ArcMAP from Louisiana (25 x 25 m grid cell; available at www.atlas.lsu.edu) and Mississippi (10 x 10 m grid cell; available at www.maris.state.ms.us). I approximated a watershed boundary polygon upstream of the datasonde location using elevations from the LIDAR layers fine-tuned with the hydrology tools in the spatial analyst toolkit of ArcMAP. These watershed boundaries were used to extract the land use within each catchment from the 2006 National Land Cover Database (NLCD; 30 x 30 m grid cell; available at: www.csc.noaa.gov/crs/lca/gulfcoast.html). Land use from this dataset is separated into 22 land cover classes, which we grouped into larger categories to simplify the data analyses. For example, cultivated and pasture/hay land uses were grouped together as agricultural land, and deciduous, evergreen, and mixed forest were grouped as forest.

Subsequently, I estimated the percent of developed, forest, agriculture, and wetland land cover within each watershed (see Table 1).

Daily rates of GPP and ER from each site were averaged over the three days, log-transformed, and used in multiple regression analysis (MRA) and principal components regression as response variables (PROC REG, PROC FACTOR, SAS Inc., Cary, NC; SAS, 2011). Predictor variables in the regression analyses (Table 2) were chosen with stepwise selection and were validated with variance inflation factors to minimize multicollinearity. In order to reduce the dimensionality of the predictor variables, principal components derived from the predictor variables were also used as independent variables in regressions with GPP and ER (Massy, 1965). The number of principal components retained for regression was determined by scree plots and the latent root and broken stick criteria (McGarigal et al., 2000).

Results

Stream temperatures typically exceeded 25°C during the summer sampling periods, except in the smaller streams with higher canopy densities (Table 3). Turbidity rarely exceeded 25 NTUs except when rainfall events stirred up silt during the datasonde deployment period, although CMR exhibited high suspended sediment loads throughout the year (personal observation). One site (UWF) was not used in year two due to a large storm that affected diel DO curves. Specific conductance in the streams was relatively low, averaging 0.071 mS cm⁻¹, whereas pH was highly variable, ranging from 5.6 – 9.2. Ambient nutrient concentrations in the study streams were typically high, especially NH₄-N, which often exceeded 0.2 mg l⁻¹. Land use percentages in each of the watersheds averaged 2.3% for developed land use, 17.8% for agricultural land use, 18.2% for wetland use, and 56.3% for forested land use (Table 4).

Table 2 Descriptions and abbreviations of variables used in correlations, multiple regression, and principal components analyses for gross primary production (GPP) and ecosystem respiration (ER) in SAS.

Predictor Variable	SAS Abbreviation	Description
Watershed Area (Ha)	WSArea	Calculated in ArcMAP 9.3 using LIDAR DEMs
Stream Order	order	Strahler stream order (Strahler, 1957)
Stream Velocity (m sec ⁻¹)	vel	Calculated from NaCl slug injection (Gordon et al., 2004)
Discharge (m ³ sec ⁻¹)	Q	Calculated from NaCl slug injection (Gordon et al., 2004)
Mean Stream Depth (cm)	depth	Mean of 30 depth measurements, 3 per transect
Mean Stream Width (m)	width	Mean of 10 wetted width measurements
Percent Algal Cover	PAlgae	Mean of 10 visual estimations of 50 cm on each side of transect
Temperature (°C)	temp	Averaged over 3-day deployment of YSI-6600EDS datasonde
Turbidity (NTU)	turb	Averaged over 3-day deployment of YSI-6600EDS datasonde
Specific Conductance (mS/cm)	SpCond	Averaged over 3-day deployment of YSI-6600EDS datasonde
Canopy Openness (%)	GLA	Calculated from Gap Light Analyzer v 2 (Frazer et al., 1999)
Nitrate-Nitrogen (mg l ⁻¹)	NO3	Analyzed colorimetrically (APHA, 2005)
Ammonium-Nitrogen (mg l ⁻¹)	NH4	Analyzed colorimetrically (APHA, 2005)
Phosphate-Phosphorus (mg l ⁻¹)	PO4	Analyzed colorimetrically (APHA, 2005)
pH	pH	Averaged over 3-day deployment of YSI-6600EDS datasonde
Benthic Organic Matter (%)	BOM	Calculated from ash-free dry mass
Biological Oxygen Demand (mg l ⁻¹)	BOD	Oxygen consumed over 20 days (APHA, 2005)
Large Woody Debris (m ² m ⁻²)	LWD	Surface area of LWD estimated via line-transect method (Wallace & Benke, 1984)
Heterotrophic Plate Count (ml ⁻¹)	HPC	Pour plate method (APHA, 2005)
Percent Agriculture	Ag	Land use from NLCD; sum of cultivated and pasture/hay land cover
Percent Developed Land	Dev	Land use from NLCD; sum of high, medium, low, and open developed land cover
Percent Forested Land	For	Land use from NLCD; sum of deciduous, evergreen, and mixed forest
Percent Wetland	Wetl	Land use from NLCD; sum of palustrine forest, scrub/shrub, and emergent wetland

Table 3 Physicochemical attributes and nutrient concentrations (\pm sd) for each of the study streams. Temperature, turbidity, specific conductance, and pH are the 3-day mean recorded by the datasondes during deployment. Nutrient concentrations were analyzed colorimetrically (APHA, 2005).

Year	Stream	Temp (°C)	Turbidity (NTU)	Specific Conductance (mS cm ⁻¹)	pH	NO ₃ -N (mg l ⁻¹)	NH ₄ -N (mg l ⁻¹)	PO ₄ -P (mg l ⁻¹)
2007	ALX	26.3 (2.4)	40.4 (4.3)	0.072 (0.003)	6.3 (0.1)	0.012 (0.013)	1.08 (0.01)	0.202 (0.011)
	BGF	23.3 (0.7)	0.3 (0.2)	0.028 (0.001)	5.8 (0)	0.017 (0.001)	0.27 (0.02)	0.084 (0.004)
	BGL	24.3 (0.8)	1.2 (0.4)	0.023 (0.002)	5.6 (0.1)	0.019 (0.001)	0.19 (0.01)	0.038 (0.009)
	BSA	28.3 (2.9)	7.8 (8.6)	0.096 (0.002)	8.0 (0.5)	0.032 (0.006)	0.46 (0.01)	0.104 (0.007)
	BVR	25.3 (2.3)	7.0 (5.6)	0.046 (0.001)	7.1 (0.5)	0.127 (0.011)	0.087 (0.025)	0.024 (0.012)
	CLR	26.4 (0.9)	3.9 (2.0)	0.039 (0.003)	6.2 (0.1)	0.108 (0.008)	0.113 (0.012)	0.061 (0.005)
	CMR	25.1 (0.7)	56.2 (5.9)	0.043 (0.006)	5.9 (0.1)	0.077 (0.010)	0.233 (0.015)	0.107 (0.013)
	DAR	25.0 (1.4)	14.6 (9.2)	0.025 (0.003)	6.4 (0.2)	0.014 (0.006)	0.113 (0.032)	0.047 (0.015)
	DNC	27.3 (0.8)	4.2 (3.9)	0.035 (0.004)	5.9 (0)	0.014 (0.007)	0.213 (0.032)	0.037 (0.007)
	LBS	27.6 (2.8)	14.9 (13.1)	0.205 (0.007)	7.8 (0.1)	0.010 (0.001)	1.533 (0.021)	0.202 (0.040)
	MWF	29.8 (2.7)	10.0 (4.9)	0.087 (0.003)	7.5 (0.7)	0.006 (0.002)	0.117 (0.015)	0.045 (0.034)
	NTL	25.6 (1.0)	25.2 (6.2)	0.097 (0.001)	6.5 (0.1)	0.115 (0.002)	0.28 (0.02)	0.204 (0.004)
	PLC	26.2 (2.1)	34.5 (13.3)	0.152 (0.005)	7.2 (0.1)	0.121 (0.014)	0.103 (0.006)	0.180 (0.012)
	SND	24.9 (0.6)	11.1 (1.0)	0.048 (0.000)	5.8 (0)	0.024 (0.019)	0.307 (0.025)	0.134 (0.054)
	TCH	22.8 (0.5)	2.3 (1.1)	0.036 (0.003)	6.0 (0.1)	0.250 (0.062)	0.24 (0.01)	0.115 (0.010)
	TMP	30.1 (3.0)	22.6 (3.5)	0.083 (0.002)	7.9 (0.5)	0.005 (0.003)	0.067 (0.012)	0.030 (0.017)
	UWF	27.7 (1.5)	16.6 (9.3)	0.100 (0.006)	7.2 (0.2)	0.044 (0.004)	0.137 (0.006)	0.065 (0.014)
2008	ALX	24.6 (2.1)	11.7 (5.1)	0.068 (0.003)	6.7 (0.2)	0.012 (0.006)	0.173 (0.031)	0.066 (0.008)
	AMT	28.5 (1.2)	5.1 (4.3)	0.048 (0.005)	7.0 (0.2)	0.003 (0.003)	0.143 (0.012)	0.053 (0.004)
	BGF	23.9 (0.9)	9.1 (3.6)	0.036 (0.002)	7.4 (0.4)	0.016 (0.006)	0.15 (0.017)	0.093 (0.005)
	BGL	24.8 (0.9)	0.9 (1.9)	0.023 (0.004)	6.6 (0.1)	0.006 (0.002)	0.187 (0.015)	0.077 (0.013)
	BSA	25.2 (1.3)	3.0 (0.5)	0.122 (0.002)	8.3 (0.5)	0.015 (0.004)	0.303 (0.006)	0.126 (0.013)
	BVR	24.5 (1.6)	6.5 (0.7)	0.051 (0.003)	7.5 (0.4)	0.117 (0.010)	0.153 (0.006)	0.079 (0.015)
	CLR	24.4 (0.9)	1.3 (0.5)	0.038 (0.003)	6.7 (0.2)	0.108 (0.012)	0.15 (0.04)	0.086 (0.015)
	CMR	26.0 (0.6)	22.7 (8.4)	0.065 (0.002)	7.3 (0.3)	0.043 (0.033)	0.293 (0.006)	0.099 (0.018)
	DAR	24.8 (1.2)	7.1 (3.1)	0.038 (0.005)	7.5 (0.2)	0.019 (0.009)	0.38 (0.046)	0.084 (0.024)
	DNC	25.6 (0.6)	1.9 (7.8)	0.035 (0.002)	6.5 (0.1)	0.018 (0.002)	0.203 (0.025)	0.08 (0.021)
	LAW	25.7 (1.2)	5.3 (2.1)	0.039 (0.002)	6.5 (0.1)	0.400 (0.100)	0.253 (0.006)	0.067 (0.010)
	LBS	26.2 (2.0)	2.9 (8.1)	0.213 (0.006)	8.1 (0.5)	0.005 (0.005)	0.103 (0.012)	0.119 (0.034)
	LWF	27.0 (2.0)	9.3 (1.6)	0.105 (0.003)	7.7 (0.5)	0.003 (0.006)	0.167 (0.021)	0.049 (0.007)
	MWF	25.2 (1.9)	12.5 (4.3)	0.124 (0.003)	7.7 (0.4)	0.017 (0.003)	0.207 (0.012)	0.086 (0.018)
	NTL	25.7 (1.1)	16.7 (9.5)	0.104 (0.002)	9.2 (0.4)	0.050 (0.004)	0.31 (0.017)	0.099 (0.008)
	PLC	25.0 (1.5)	12.1 (19.2)	0.166 (0.006)	7.6 (0.1)	0.077 (0.027)	0.14 (0.017)	0.146 (0.028)
	PSH	26.1 (1.3)	1.4 (2.0)	0.045 (0.005)	8.2 (0.5)	0.084 (0.005)	0.123 (0.012)	0.045 (0.005)
SND	25.5 (0.7)	15.1 (1.8)	0.067 (0.003)	6.8 (0.2)	0.045 (0.009)	0.487 (0.04)	0.158 (0.009)	
SSC	24.3 (0.9)	15.6 (1.4)	0.036 (0.003)	6.2 (0.1)	0.103 (0.021)	0.11 (0.01)	0.113 (0.017)	
TCH	23.5 (0.4)	2.9 (1.2)	0.039 (0.002)	7.1 (0.2)	0.235 (0.017)	0.177 (0.006)	0.125 (0.013)	
TCK	24.0 (1.2)	1.9 (0.4)	0.034 (0.002)	7.1 (0.1)	0.065 (0.007)	0.147 (0.006)	0.08 (0.008)	
TMP	27.1 (2.1)	2.7 (0.3)	0.092 (0.004)	7.7 (0.3)	0.003 (0.006)	0.243 (0.012)	0.058 (0.022)	
TNG	26.3 (1.0)	9.1 (3.2)	0.055 (0.004)	7.2 (0.1)	0.092 (0.006)	0.113 (0.006)	0.111 (0.017)	

GPP rates ranged from 0.06 – 7.90 g O₂ m⁻² d⁻¹, with a mean of 0.84 g O₂ m⁻² d⁻¹ in 2007 and 1.84 g O₂ m⁻² d⁻¹ in 2008 (Table 5; Fig. 2a). ER rates, expressed as negative values as they represent a loss of DO from the stream, were -0.23 to -11.07 g O₂ m⁻² d⁻¹ and averaged -2.77 g O₂ m⁻² d⁻¹ in 2007 and -3.56 g O₂ m⁻² d⁻¹ in 2008. Net daily metabolism calculations indicated

Table 4 Watershed area above datasonde and percentage of developed, agricultural, wetland, and forested land use listed for each stream. Watershed areas were calculated in ArcGIS 9.3 and land use data was taken from 2006 National Land Cover Database.

Stream	Watershed Area (ha)	Dev (%)	Ag (%)	Wetl (%)	For (%)
ALX	6015.74	2.26	27.46	36.39	28.85
AMT	145643.04	1.94	12.51	17.06	62.43
BGF	6121.24	1.27	6.34	16.59	63.69
BGL	5210.40	2.23	12.98	24.15	52.13
BSA	17561.20	1.67	5.85	4.34	84.26
BVR	2816.59	0.60	26.04	11.27	57.22
CLR	1587.17	1.20	13.22	29.10	52.99
CMR	20048.34	1.74	21.20	27.23	44.11
DAR	16874.19	1.64	7.40	21.12	64.44
DNC	1177.78	1.27	11.58	21.19	61.79
LAW	13164.15	2.29	20.85	26.37	43.42
LBS	8789.77	1.33	7.11	3.21	84.93
LWF	9231.13	3.16	25.93	9.76	55.35
MWF	6903.01	4.05	28.49	9.54	51.50
NTL	14306.75	5.53	21.48	26.03	39.52
PLC	1451.48	0.24	0.30	1.29	97.82
PSH	33316.05	1.85	25.19	20.10	47.85
SND	5369.87	1.47	19.64	34.09	40.15
SSC	11516.92	2.38	29.15	18.71	45.24
TCH	5109.96	2.00	30.18	23.11	39.64
TCK	22799.67	1.99	15.26	16.88	60.27
TMP	10605.04	0.97	10.46	10.13	73.48
TNG	62539.71	7.25	20.00	18.80	48.87
UWF	2897.62	5.54	27.39	10.02	50.73

heterotrophic conditions at all sites except BVR and DAR in 2007 and PLC, LBS, TMP, LAW in 2008 (Fig. 2b). Reaeration values varied from 1.01 d^{-1} in ALX, which exhibited some of the lowest velocity and discharge rates recorded during the study, to 36.12 d^{-1} in BVR, which, despite being a relatively small 2nd order system, had the greatest slope and one of the highest velocities among the study streams. Reaeration values calculated in 2009 with EDM were generally in agreement with reaeration measured directly through propane-solute injections ($R^2 = 0.34$; $p < 0.05$; $n = 13$; Fig. 3). In three of the streams, however, calculated reaeration values underestimated measured reaeration values by nearly one-third where two of these streams were the shallowest streams at less than 10 cm mean depth. However, a third stream that averaged 8

Table 5 Stream velocity, discharge, slope, temperature, reaeration (k_{O_2}), GPP ($\pm se$), and ER ($\pm se$) at each of the study sites. Reaeration is calculated via energy dissipation model (EDM) and is a function of velocity, slope, and discharge.

Year	Stream	Velocity (m sec ⁻¹)	Discharge (m ³ sec ⁻¹)	Slope (m m ⁻¹)	k_{O_2} (d ⁻¹)	GPP (g O ₂ m ⁻² d ⁻¹)	ER (g O ₂ m ⁻² d ⁻¹)
2007	ALX	0.025	0.024	0.00141	1.01	0.271 (0.09)	0.306 (0.11)
	BGF	0.064	0.200	0.00117	2.13	0.357 (0.04)	2.812 (0.02)
	BGL	0.060	0.109	0.00208	3.56	0.322 (0.11)	4.922 (2.10)
	BSA	0.303	0.431	0.00170	10.97	0.297 (0.08)	2.190 (0.29)
	BVR	0.333	0.104	0.00268	25.28	1.479 (0.14)	1.190 (0.12)
	CLR	0.031	0.051	0.00213	1.89	0.463 (0.02)	1.115 (0.05)
	CMR	0.185	0.679	0.00240	6.79	0.506 (0.91)	11.067 (0.58)
	DAR	0.230	0.548	0.00192	9.38	2.150 (0.36)	1.364 (0.31)
	DNC	0.069	0.047	0.00203	3.99	0.240 (0.03)	3.163 (0.10)
	LBS	0.247	0.235	0.00152	10.61	0.062 (0.06)	0.488 (0.10)
	MWF	0.083	0.135	0.00245	5.78	2.636 (0.23)	2.832 (0.08)
	NTL	0.238	0.487	0.00138	7.00	2.525 (0.16)	3.033 (0.17)
	PLC	0.073	0.067	0.00228	4.72	0.070 (0.06)	0.238 (0.02)
	SND	0.067	0.078	0.00110	2.08	0.632 (0.08)	3.618 (0.08)
	TCH	0.187	0.346	0.00130	5.19	0.554 (0.05)	4.787 (0.13)
	TMP	0.128	0.174	0.00103	3.75	0.180 (0.61)	0.274 (0.50)
	UWF	0.111	0.092	0.00183	5.76	1.626 (0.15)	2.292 (0.06)
2008	ALX	0.076	0.008	0.00141	3.04	0.119 (0.06)	0.275 (0.01)
	AMT	0.490	5.500	0.00201	15.10	5.908 (0.54)	6.727 (0.90)
	BGF	0.068	0.144	0.00117	2.27	1.477 (0.14)	4.604 (0.14)
	BGL	0.058	0.093	0.00208	3.39	0.661 (0.03)	2.505 (0.07)
	BSA	0.303	0.491	0.00170	10.97	0.595 (0.02)	3.373 (0.15)
	BVR	0.476	0.143	0.00268	36.12	0.805 (0.07)	2.021 (0.36)
	CLR	0.077	0.031	0.00213	4.63	0.659 (0.04)	1.072 (0.18)
	CMR	0.171	0.422	0.00240	8.73	0.973 (0.01)	8.270 (0.05)
	DAR	0.215	0.465	0.00192	8.78	3.964 (0.60)	4.587 (0.2)
	DNC	0.078	0.026	0.00203	4.47	0.080 (0.02)	2.984 (0.05)
	LAW	0.370	0.526	0.00194	15.34	7.904 (0.26)	6.403 (0.37)
	LBS	0.196	0.138	0.00152	8.42	0.280 (0.05)	0.234 (0.04)
	LWF	0.119	0.225	0.00157	5.28	0.858 (0.09)	1.586 (0.07)
	MWF	0.175	0.104	0.00245	12.18	1.895 (0.05)	2.088 (0.10)
	NTL	0.139	0.201	0.00138	5.42	1.318 (0.04)	2.844 (0.02)
	PLC	0.203	0.035	0.00228	13.10	1.217 (0.08)	0.251 (0.11)
	PSH	0.741	1.482	0.00227	25.77	6.681 (0.20)	8.963 (0.53)
	SND	0.049	0.033	0.00110	1.53	0.195 (0.01)	2.243 (0.06)
	SSC	0.303	0.369	0.00104	6.72	1.193 (0.24)	5.481 (0.14)
	TCH	0.181	0.218	0.00130	6.66	0.482 (0.07)	6.536 (0.15)
TCK	0.222	0.678	0.00132	4.47	0.716 (0.04)	2.551 (0.23)	
TMP	0.147	0.159	0.00103	4.31	1.058 (0.13)	0.536 (0.09)	
TNG	0.404	2.947	0.00099	6.09	3.294 (0.35)	5.648 (0.19)	

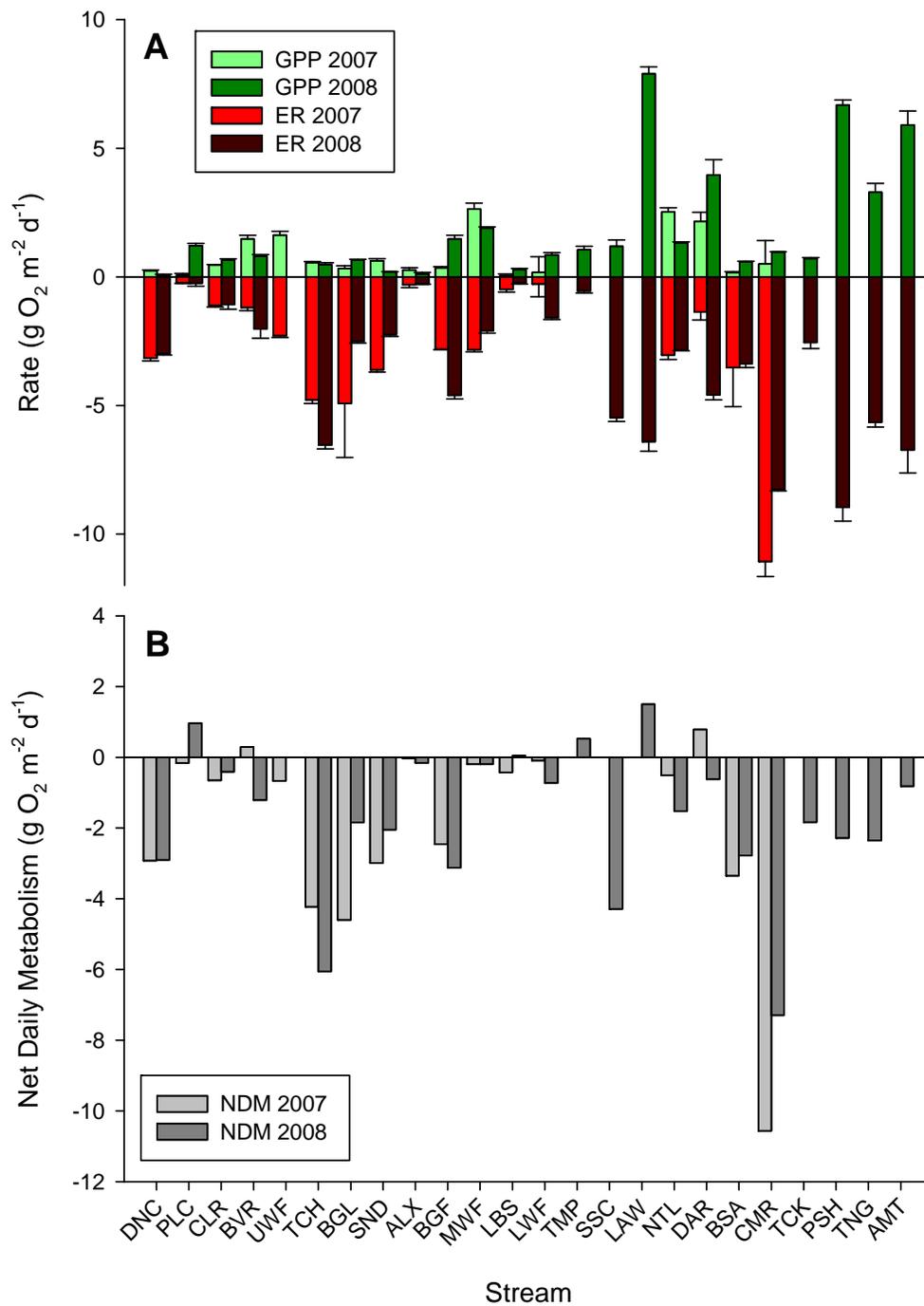


Fig. 2 Rates of (a) gross primary production (GPP; positive values), ecosystem respiration (ER; negative values), and (b) net daily metabolism in 2007 and 2008 at each study site, arranged along a gradient of watershed size with DNC having the smallest watershed and AMT the largest

cm deep over-estimated reaeration by 34%, but this stream had one of the highest velocities. Most of the stream size variables, such as watershed area, velocity, discharge, depth, and width, were highly correlated (Table 6), but none of these variables, including discharge, were correlated with reaeration.

Overall, GPP was positively correlated with $\text{NO}_3\text{-N}$ concentrations, and tended to increase with stream size, increasing canopy openness, and many of the other stream size variables, especially width (Table 6). Similarly, ER was also correlated with many of the variables associated with stream size (Table 7), as well as LWD. Although BOM was correlated with both LWD and negatively correlated with BOD, and HPC was correlated with $\text{PO}_4\text{-P}$ and $\text{NH}_4\text{-N}$ levels, ER was not related to BOM, BOD, or HPC, all of which were measured as indicators of the potential amount of organic matter available to heterotrophs. Among the land-use variables, percent agriculture was correlated with stream nitrate concentrations (Table 8). Percent forested land, which decreased in the watersheds as agricultural or developed land use increased, was positively correlated with ER and pH but negatively correlated with LWD.

After accounting for multicollinearity (e.g., variance inflation factors [vif], tolerances, and condition indices) and performing regressions with stepwise, forward, and backward selections of predictor variables, the final model accounted for 70% of the variation in GPP and was positively associated with canopy openness (GLA; 36% of the variation), mean depth (depth; 18% of the variation), and percent agriculture in the watershed (Ag; 9% of the variation), and negatively associated with ammonium ($\text{NH}_4\text{-N}$; 7% of the variation) levels ($R^2 = 0.70$, $p < 0.01$, $n=40$; Table 9). The ER model explained 80% of the variation in the data and was

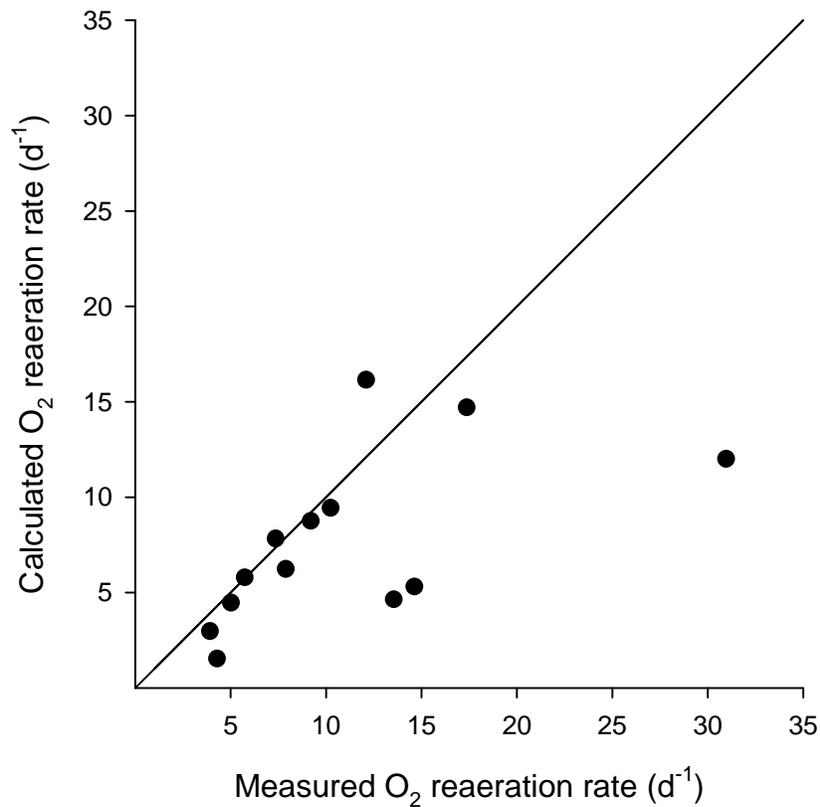


Fig. 3 Except for the shallowest streams, reaeration rates measured via propane evasion were generally in agreement with reaeration estimated by the energy dissipation model of Tsvoglo and Neal (1976) in 2009 ($R^2 = 0.034$; $p < 0.05$; $n = 13$). Diagonal line represents 1:1 line for comparison.

positively associated with depth (46% of the variation), while stream velocity (vel), discharge (Q), BOD, percent developed land in the watershed (Dev), and specific conductance (SpCond) accounted for the remaining 31% of the variation ($R^2 = 0.77$, $p < 0.01$, $n=40$; Table 9). Variance inflation factors and condition index diagnostics did not indicate multicollinearity in the models, although depth and Q may have been weakly dependent as condition indices were approaching 10 (SAS, 2011).

Table 6 Pearson correlation coefficients for variables traditionally correlated with gross primary production (GPP). Only significant correlations are reported (— = not significant). See Table 2 for abbreviations.

	GPP	WSArea	vel	Q	depth	width	GLA	NO3	NH4	PO4	PAlgae	turb	pH
GPP	1	.55	.67	.58	.42	.46	.66	.38	—	—	—	—	—
WSArea		1	.54	.99	.65	.83	.43	—	—	—	—	—	—
vel			1	.58	—	.54	.62	—	—	—	—	—	.34
Q				1	.66	.81	.40	—	—	—	—	—	—
depth					1	.47	—	—	—	—	—	—	—
width						1	.55	—	—	—	—	—	—
GLA							1	—	—	—	—	—	.51
NO3								1	—	—	—	—	—
NH4									1	.71	—	—	—
PO4										1	—	.52	—
PAlgae											1	.38	—
turb												1	—

Table 7 Pearson correlation coefficients for variables traditionally correlated with ecosystem respiration (ER). Only significant correlations are reported (— = not significant). See Table 2 for abbreviations.

	ER	vel	Q	depth	width	BOM	BOD	LWD	HPC	NO3	NH4	PO4	pH
ER	1	.44	.43	.68	.32	—	—	.39	—	—	—	—	—
vel		1	.58	—	.54	-.34	—	-.32	—	—	—	—	.34
Q			1	.66	.82	—	—	—	—	—	—	—	—
depth				1	.47	.34	—	.49	—	—	—	—	—
width					1	—	—	—	—	—	—	—	—
BOM						1	-.37	.67	—	—	—	—	-.33
BOD							1	—	—	—	—	—	—
LWD								1	—	—	—	—	-.51
HPC									1	—	.63	.46	—
NO3										1	—	—	—
NH4											1	.71	—
PO4												1	—

Table 8 Pearson correlation coefficients for land use variables, water quality attributes, and ecosystem metabolism rates. Only significant correlations are reported (— = not significant). See Table 2 for abbreviations.

	Ag	Dev	For	Wetl	NO3	NH4	PO4	turb	PAlgae	LWD	BOM	HPC	BOD	pH	GPP	ER
Ag	1	.46	-.82	.41	.32	—	—	—	—	—	—	—	—	—	—	—
Dev		1	-.44	—	—	—	—	—	.33	—	—	—	—	—	—	—
For			1	-.83	—	—	—	—	—	-.34	—	—	—	.40	—	-.39
Wetl				1	—	—	—	—	—	.45	—	—	—	-.56	—	—
NO3					1	—	—	—	—	—	—	—	—	—	.38	—
NH4						1	.71	—	—	—	—	.63	—	—	—	—
PO4							1	.52	—	—	—	.46	—	—	—	—
turb								1	.38	—	-.35	.37	—	—	—	—
PAlgae									1	-.42	—	.41	—	—	—	—
LWD										1	.67	—	—	-.51	—	.39
BOM											1	—	-.37	-.33	—	—
HPC												1	—	—	—	—
BOD													1	—	—	—
pH														1	—	—
GPP															1	.48

Table 9 Summary statistics for significant predictors in multiple regression analyses of gross primary production and ecosystem respiration.

Dependent Variable	Independent Variable	Coefficient	p-value	Variance Inflation Factor ^a
log(GPP)	Intercept	-2.959	< 0.0001	0
	GLA	0.0316	< 0.0001	1.0002
	depth	0.0236	0.0002	1.0489
	Ag	0.0379	0.0047	1.0090
	NH4	-1.193	0.0089	1.0513
log(ER)	Intercept	-1.8295	0.0027	0
	depth	0.0410	< 0.0001	3.0081 ^b
	vel	3.5761	< 0.0001	1.6995
	Q	-0.6524	0.0007	3.3736 ^b
	BOD	0.1598	0.0157	1.0776
	Dev	0.2304	0.0008	1.0841
	SpCond	-7.4039	0.0045	1.6015

^aVariance Inflation Factors (vif) are considered high when $vif > 10$ or $vif > 1/(1-R^2)$

^bModerate vif

In the principal component (PC) analysis, four components were retained from scree plots and the latent root and broken stick criteria (Table 10). Analyses indicated that PC1 (22.4% of the variance explained) was heavily influenced by stream size variables, exhibiting positive associations with watershed area, stream order, discharge, water velocity, depth, width, and canopy openness. In contrast, PC2 (18.1%) was positively associated with depth, LWD, and percent wetland in the watershed, and negatively associated with stream order, velocity, canopy openness, algal cover, pH, specific conductance, and percent forest in the watershed. The 3rd PC (14%) was positively associated with algal cover and 3 of the 4 landscape variables, and

Table 10 Loadings of variables and percent variance explained on first four axes of principal components analysis

Variable	Principal component axis			
	Factor 1	Factor 2	Factor 3	Factor 4
WSArea	0.95	—	—	—
order	0.71	-0.30	—	—
Q	0.94	—	—	—
vel	0.62	-0.31	—	—
depth	0.67	0.62	—	—
width	0.91	—	—	—
PAlgae	—	-0.35	0.44	—
GLA	0.55	-0.61	—	—
NO3	—	—	—	—
NH4	—	—	—	0.93
PO4	—	—	—	0.79
pH	—	-0.79	—	—
BOM	—	—	—	—
BOD	—	—	—	—
LWD	—	0.85	—	—
HPC	—	—	—	0.77
Ag	—	—	0.86	—
Dev	—	—	0.71	—
For	—	-0.46	-0.86	—
Wetl	—	0.67	0.54	—
turb	—	—	—	0.31
SpCond	—	-0.74	—	—
% variance explained	22.4	18.1	13.9	9.5

For clarity, only loadings >0.3 are shown

negatively correlated with percent forest, whereas PC4 (9.5%) was positively associated with PO₄-P, NH₄-N, HPC, and turbidity. Together, PC1, PC2, and PC4 explained 57% of the variation in the regression with GPP ($p < 0.01$, $n=40$; Table 11), whereas only PC2 was significantly related to ER, explaining 53% of the variation in the data ($p < 0.01$, $n=40$; Table 10).

Table 11 Summary statistics for significant principal components in multiple regression analyses of gross primary production (GPP; $R^2 = 0.57$, $p < 0.01$, $n=40$) and ecosystem respiration (ER; $R^2 = 0.53$, $p < 0.01$, $n=40$)

Dependent Variable	Coefficient	Independent Variable	p-value
log(GPP)	-0.3138	Intercept	0.0224
	0.5415	PC1	0.0002
	0.6171	PC2	< 0.0001
	-0.3973	PC4	0.0051
log(ER)	0.7107	Intercept	< 0.0001
	0.8051	PC2	< 0.0001

Discussion

Observed rates of GPP and ER were similar to those presented in previous studies across multiple biomes (Sinsabaugh, 1997; Lamberti and Steinman, 1997; Mulholland et al., 2001; Bernot et al., 2010; Frankforter et al., 2010), or within single biomes across disturbance (Houser et al., 2005) or land use gradients (McTammany et al., 2007; Izagirre et al., 2008; Hagen et al., 2010). My findings agreed with previous studies that light availability in wider streams was the most dominant factor regulating GPP, with other factors either promoting or limiting GPP rates, subject to influences from watershed activities. In turn, ER was most strongly related to the presence of OM, usually derived from the canopy in narrower streams while being augmented by autotrophic respiration in larger systems.

Sunlight has been cited as a major controlling factor of GPP, measured via PAR or approximated by canopy cover and/or stream width (Young et al., 2008; Tank et al., 2010). My results also indicate that stream size was one of the dominant controls of GPP, as at least one variable associated with stream size corresponded to higher GPP rates in each of the statistical analyses. For both Pearson correlations and PCA, watershed size, stream discharge, stream

width, stream depth, and canopy openness were significant correlates of GPP. For the MRA, canopy openness and depth were significant predictors of GPP related to stream size. A relationship with depth seems counterintuitive, but depth may be a surrogate measure for other stream size variables, and was included in the final model due to minimal variance inflation. The deepest stream, at just under 1 m, still had some of the highest rates of GPP, and may not have been deep enough to prevent light from reaching the sediments. Additionally, I observed that shallower streams tended to have more mobile sediments during spates, and mobile sediments have been shown to scour algae (Peterson, 1996) and depress rates of GPP (Atkinson et al., 2008). Some of the deeper streams had more gravel sediments that tended to be more stable and were able to resist moderate increases in discharge, which appeared to allow sustained growth of algae. The PCA revealed that the study sites fell into two groups that varied along a gradient of stream size and decreased canopy cover. In addition, a few of the sites with higher GPP were in some of the largest streams that were characterized by lower velocities and high levels of large LWD (Fig. 4). LWD may have been particularly important to GPP in these streams by providing increased surface areas of stable substrate for algal colonization (Hoellein et al., 2009).

Other important factors associated with increased GPP rates included $\text{NO}_3\text{-N}$, percent agricultural land use, and increased percent wetland and decreased percent forestry, the latter of which appeared to be related to the increase in agricultural and developed land uses. Increased concentrations of nitrate and other nutrients have been commonly seen in lotic systems within agriculturally-developed watersheds (Goolsby et al., 2001; Kemp and Dodds, 2001; Vanni et al., 2001) and have been attributed to increased rates of GPP (Wiley et al., 1990; McTammany et al., 2007; Frankforter et al., 2010) and the development of net autotrophic conditions (Wiley et al., 1990; Bunn et al., 1999; Young and Huryn, 1999). I observed similar results as nitrate

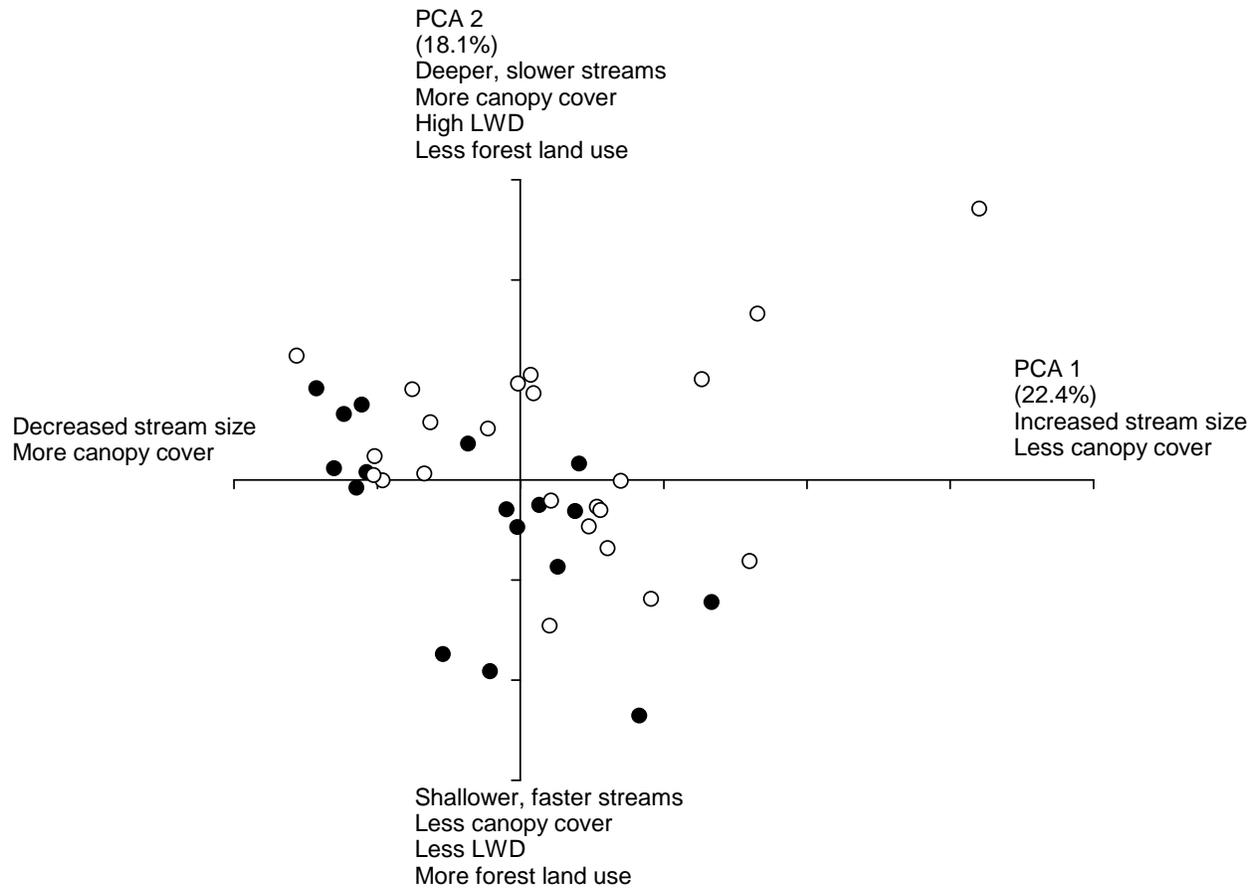


Fig. 4 Results of the principal components analysis for study streams, shown only for the first two axes. Closed circles (●) are 2007 while open circles (○) are 2008. Gross primary production (GPP) generally increases moving from the top-left quadrant to the bottom right quadrant. However, a few of the largest and deepest streams in the top-right quadrant had some of the highest rates of GPP.

concentrations were positively correlated with percent agricultural land use in the watershed (Table 7). However, $\text{NO}_3\text{-N}$ did not have any significant correlations with any of the principal components, nor was it a significant predictor in MRA, although the latter could be due to its correlation with percent agriculture and its removal from the final model due to variance inflation.

Interestingly, ammonium was a negative predictor of GPP in MRA in the study streams, although increased $\text{NH}_4\text{-N}$ has been reported to be positively correlated with GPP in other

studies (Bernot et al., 2010), with increased ammonium uptake being reflected in higher GPP and ER rates (Hall and Tank, 2003; Webster et al., 2003). However, ammonium concentrations in some of the streams in this study were as much as 2 to 3 orders of magnitude higher than those reported in the studies mentioned above. Although ammonium concentrations rarely exceed nitrate concentrations in lotic systems, there have been several cases where it has occurred, especially in Gulf and Atlantic coastal states (Stanley and Ward, 1997; Clark et al., 2000 and appendices; NCASI, 2001; Webster et al., 2003; D.G. Kelly, LSU AgCenter, unpublished data). Exceedingly high ammonium concentrations can be toxic, or can severely limit primary production in both marine algae (Kautsky, 1982; Tamminen, 1982) and wetland plants (Clarke and Baldwin, 2002). Increased ammonium concentrations may have been related to low DO conditions upstream of the study reach, an indication of stream impairment, or increased interaction with the hyporheos, although the latter would seem less likely since hyporheic exchange is generally considered low in sandy streams (Stofelth et al., 2008).

Similar to GPP, ER was positively correlated with many of the stream size variables as well as GPP and the surface area of submerged LWD. Generally, ER rates are fueled by allochthonous OM in smaller systems and autochthonous production in larger systems (Young et al., 2008; Tank et al., 2010). With a few exceptions, GPP rates were low in the smaller systems, so BOM and LWD derived from the canopy or surrounding riparian forest were likely fueling ER in this study. However, in the larger systems autotrophic respiration was likely an important component of ER, as reported in previous studies (Wiley et al., 1990; McTammany et al., 2007) or autotrophic OM production is fueling heterotrophic respiration. In MRA, there were several variables that were significant predictors of ER, including stream size variables, BOD, percent developed land, and specific conductance. In these systems, increased developed land could be

contributing to an increased level of BOD as well as increased ER via organic pollution (Bott et al., 2006; Izagirre et al., 2008).

Regression analyses indicated that ER was significantly related to PC2 (Fig. 5; Table 10), but not PC1, which was predominately described by stream size variables such as width, depth, discharge, velocity, and canopy openness. The gradient along PC2 contrasted shallower, faster streams with less canopy cover and low woody debris abundance to deeper, slower streams with more canopy cover and LWD. As with previous studies, ER did not necessarily change along a size continuum (McTammany et al., 2003), but did increase with GPP, suggesting that the decrease in respiration related to decomposition of allochthonous OM from the canopy in smaller systems was offset by concomitant increases in algal respiration, decomposition, or algal-derived OM production in larger streams (McTammany et al., 2007).

My results agree with previous reports that small forested streams are typically dominated by net heterotrophic conditions (Meyer and Webster, 1997), as most of the smaller study streams were largely net heterotrophic with low GPP. If I use watershed area as a proxy for stream size measurements (Fig. 2), the general trend of increasing metabolism rates with increasing stream size matches the findings of previous studies where rates of GPP (and sometimes ER) increased in downstream reaches (Bott et al., 1985; Naiman et al., 1987; Minshall et al., 1992; McTammany et al., 2003). Many of these studies found that GPP rates increased in excess of ER rates, or that ER rates stayed about the same as stream order increased, resulting in the development of net autotrophy in the mid-order reaches (e.g., 4th – 7th). Although I did not observe the transition from predominately heterotrophic to predominately autotrophic conditions, the largest of the study streams was only 4th order.

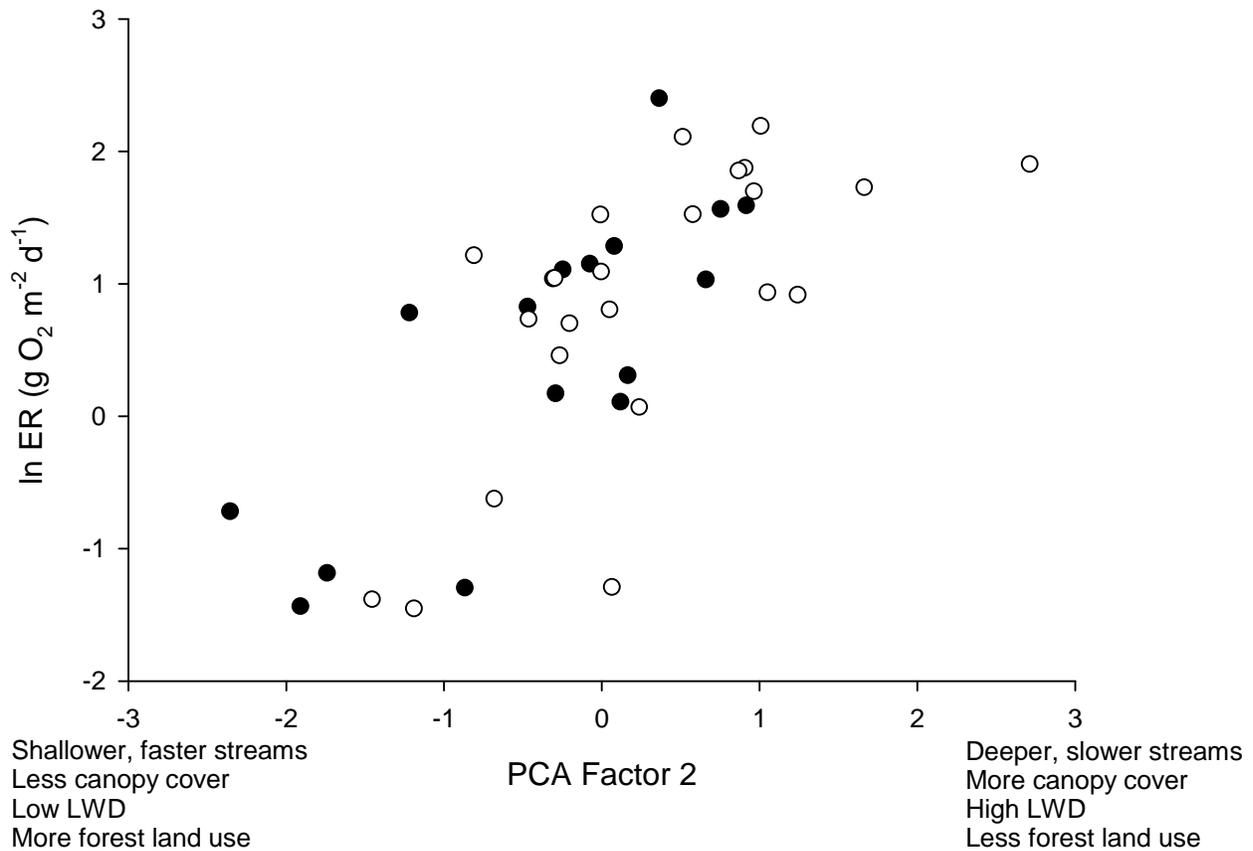


Fig. 5 Ecosystem respiration (ER) rates increased with PCA factor 2, from shallower, faster streams with low LWD and low canopy cover to deeper, slower streams with high LWD and more canopy cover. Closed circles (●) are 2007 while open circles (○) are 2008.

Several studies have analyzed the effect of land use and/or watershed disturbance on rates of ecosystem metabolism. Increased agricultural activities within the watershed have been implicated in increased nutrient concentrations in streams and increased rates of GPP (McTammany et al., 2007; Izagirre et al., 2008; Bernot et al., 2010; Hagen et al., 2010). Moreover, net autotrophic conditions can occur in agriculturally dominated systems due to GPP increases as nutrient inputs rise (Young and Huryn, 1999; Wiley et al., 1990; Bunn et al., 1999). However, agricultural activity has also been connected to increased stream turbidity, resulting in

reduced GPP rates (Young and Huryn, 1999; Hagen et al., 2010). Analyses of my data indicated that increased agricultural land use was related to increased concentrations of $\text{NO}_3\text{-N}$ and increased GPP, although this was not reflected in the PCA. The latter finding may be related to the increased importance of stream size variables in the analyses, which could have overshadowed influences of nutrient additions on GPP rates. These results are similar to Hill et al. (2009), who reported that light was approximately 10 times more important than nutrients in describing changes in GPP rates. Consequently, although increased nutrients from agricultural activity was an important factor influencing GPP rates in similar-sized streams with seemingly similar light regimes, light availability in the larger streams was a more important regulator of GPP rates.

Land use activities have also been implicated as important factors influencing variation in ER rates. For example, agricultural activities can influence respiration by stimulating GPP, with the resulting autotrophic respiration, decomposition, or algal derived OM production being major components of ER (Bunn et al., 1999; Young and Huryn, 1999; McTammany et al., 2007). Likewise, both Izagirre et al. (2008) and Bott et al. (2006) found increased ER rates in streams with increasing urban and industrial developed land use and attributed the increase to the input of organic pollution from sources such as sewers or industrial pollution. Houser et al. (2005) found that ER was positively correlated with the amount of LWD in the stream, with increased upland disturbance resulting in a depletion of LWD, usually by sediment burial. Interestingly, ER was inversely correlated with percent forested land in the watershed in this study, which is contrary to the results of previous studies (Bernot et al., 2010). However, land use closest to the stream (i.e., within the river corridor or subcorridor) may be more important in determining rates of ecosystem metabolism (McTammany et al., 2007), leaf breakdown (Sponseller and Benfield,

2001), and macroinvertebrate assemblages in forested streams (Sponsellor et al., 2001). Hence the influences of land use on stream metabolism may be a function of scale and proximity to the stream, perhaps requiring a multi-scale weighted approach to analyses.

Reaeration rates calculated for my study streams were lower than those reported in other studies (e.g., Mulholland et al., 2001; Acuña et al., 2004; Houser et al., 2005). However, EDM estimates in my study streams compared well with k_{O_2} values measured from propane evasion and were within the range I expected from these laminar-flowing, low-gradient coastal plain streams as EDM reaeration models were developed for low-gradient coastal plain streams in Georgia (Tsviglo and Neal, 1976). Mulholland et al. (2001) reported that shallow streams tend to result in underestimation of actual reaeration rates, which was apparent in a few of the shallowest systems that I studied, and may have led to some errors in the calculations of ecosystem metabolism rates. Shallower streams have a higher surface-area to water volume ratio and thus have more exposure of surface water to allow greater exchange of atmospheric gases or possibly more vertical mixing, and EDM models may not be the most appropriate empirical models for calculating reaeration in these systems.

Overall, ecosystem metabolism in these coastal plain streams appeared to behave similarly to other systems reported in the literature, with GPP rates increasing in larger systems and ER rates remaining relatively constant. Few of the larger systems may have become highly net autotrophic, but this may be due to the lack of streams greater than 4th order in size, and only two 4th order streams were used in this study. Nutrients both stimulated (e.g., NO_3-N from agricultural) and depressed (i.e., high concentrations of NH_4-N) GPP, and although I was unable to determine the direct effect of heterotrophic bacteria on ER, I did see evidence that urban development may lead to increased respiration rates. Consequently, my comparisons of GPP and

ER in many systems over a spatially limited area may have identified several potentially impaired streams worth further study; however, further studies would help to further elucidate streams in Louisiana as possibly impaired or as streams in this area naturally exist. In conclusion, streams in Louisiana have rarely been studied and represent a rich area for research. For example, high NH₄-N concentrations have only been reported in a few areas and the mechanisms for these high concentrations are unknown. Additionally, year to year variability in these streams can be high with the possibility of aberrant weather conditions occurring from global climate change (e.g., increased hurricanes, drought; Hanson et al., 2012) and the effects of year to year variability in multiple spatial study areas has been rarely published.

References

- Acuña, V., A. Giorgi, I. Munoz, U. Uehlinger, and S. Sabater, 2004. Flow extremes and benthic organic matter shape the metabolism of a headwater Mediterranean stream. *Freshwater Biology* 49:960-971.
- Allan, J.D., 2004. Landscapes and riverscapes: the influence of land use on stream ecosystems. *Annual Review of Ecology and Systematics* 35:257-284.
- APHA (American Public Health Association), 2005. Standard methods for the examination of water and wastewater, 21st edition. American Public Health Association. Washington, DC.
- Atkinson, B.L., M.R. Grace, B.T. Hart, and K.E.N. Vanderkruk, 2008. Sediment instability affects the rate and location of primary production and respiration in a sand-bed stream. *Journal of the North American Benthological Society* 27:581-592.
- Bernot, M.J., D.J. Sobota, R.O. Hall, P.J. Mulholland, W.K. Dodds, J.R. Webster, J.L. Tank, L.R. Ashkenas, L.W. Cooper, C.N. Dahm, S. Findlay, S.V. Gregory, N.B. Grimm, S.K. Hamilton, S.L. Johnson, W.H. McDowell, J.L. Meyer, B.J. Peterson, G.C. Poole, H.M. Valett, C. Arango, J.J. Beaulieu, A.J. Burgin, C. Crenshaw, A.M. Helton, L. Johnson, J. Merriam, B.R. Niederlehner, J.M. O'Brien, J.D. Potter, R.W. Sheibley, S.M. Thomas, and K. Wilson, 2010. Inter-regional comparison of land-use effects on stream metabolism. *Freshwater Biology* 55:1874-1890.

- Biggs, B.J.F., R.A. Smith, and M.J. Duncan, 1999. Velocity and sediment disturbance of periphyton in headwater streams: biomass and metabolism. *Journal of the North American Benthological Society* 18:222-241.
- Bott, T.L., 2006. Primary production and community respiration. In: Hauer, F.R., and G.A. Lamberti, (editors), *Methods in Stream Ecology*, 2nd edition. Academic Press, Burlington, MA: 663-690.
- Bott, T.L., J.T. Brock, C.S. Dunn, R.F. Naiman, R.W. Ovink, and R.C. Petersen, 1985. Benthic community metabolism in four temperate stream systems: an inter-biome comparison and evaluation of the river continuum concept. *Hydrobiologia* 123:3-45.
- Bott, T.L., D.S. Montgomery, J.D. Newbold, D.B. Arscott, C.L. Dow, A.K. Aufdenkampe, J.K. Jackson, and L.A. Kaplan, 2006. Ecosystem metabolism in stream of the Catskill Mountains (Delaware and Hudson River watersheds) and Lower Hudson Valley. *Journal of the North American Benthological Society* 25:1018-1044.
- Bunn, S.E., P.M. Davies, and T.D. Mosisch, 1999. Ecosystem measures of river health and their response to riparian and catchment degradation. *Freshwater Biology* 41:333-345.
- Clark, G.M., D.K. Mueller, and M.A. Mast, 2000. Nutrient concentrations and yields in undeveloped stream basins of the United States. *Journal of the American Water Resources Association* 36:849-860.
- Clarke, E., and A.H. Baldwin, 2002. Responses of wetland plants to ammonia and water level. *Ecological Engineering* 18:257-264.
- Fellows, C.S., H.M. Valett, and C.N. Dahm, 2001. Whole-stream metabolism in two montane streams: contribution of the hyporheic zone. *Limnology and Oceanography* 46:523-531.
- Fisher, S.G., L.J. Gray, N.B. Grimm, and D.E. Busch, 1982. Temporal succession in a desert stream ecosystem following flash flooding. *Ecological Monographs* 52:93-110.
- Frankforter, J.D., H.S. Weyers, J.D. Bales, P.W. Moran, and D.L. Calhoun, 2010. The relative influence of nutrients and habitat on stream metabolism in agricultural streams. *Environmental Monitoring and Assessment* 168:461-479.
- Frazer, G.W., Canham, C.D., and K.P. Lertzman, 1999. Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation. Copyright © 1999: Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York: 36 pp.
- Gerull, L., A. Frossard, M.O. Gessner, and M. Mutz, 2012. Effects of shallow and deep sediment disturbance on whole-stream metabolism in experimental sand-bed flumes. *Hydrobiologia* 683:297-310.

- Goolsby, D.A., W.A. Battaglin, B.A. Aulenbach, and R.P. Hooper, 2001. Nitrogen input to the Gulf of Mexico. *Journal of Environmental Quality* 30:329-336.
- Gordon, N.D., T.A. McMahon, B.L. Finlayson, G.J. Gippel, and R.J. Nathan, 2004. *Stream Hydrology: An Introduction for Ecologists*, 2nd edition. Wiley, England: 429 pp.
- Grimm, N.B., and S.G. Fisher, 1984. Exchange between interstitial and surface water: implications for stream metabolism and nutrient cycling. *Hydrobiologia* 111:219-228.
- Hall, R.O., and J.L. Tank, 2003. Ecosystem metabolism controls nitrogen uptake in streams in Grand Teton National Park, Wyoming. *Limnology and Oceanography* 48:1120-1128.
- Hagen, E.M., M.E. McTammany, J.R. Webster, and E.F. Benfield, 2010. Shifts in allochthonous input and autochthonous production in stream along an agricultural land-use gradient. *Hydrobiologia* 655:61-77.
- Hansen, J., M. Sato, and R. Ruedy, 2012. Perception of climate change. *Proceedings of the National Academy of Sciences* 109:2415-2423.
- Hill, W.R., S.E. Fanta, and B.J. Roberts, 2009. Quantifying phosphorus and light effects in stream algae. *Limnology and Oceanography* 54:368-380.
- Hoellein, T.J., J.L. Tank, E.J. Rosi-Marshall, and S.A. Entrekin, 2009. Temporal variation in substratum-specific rates of N uptake and metabolism and their contribution at the stream-reach scale. *Journal of the North American Benthological Society* 28:305-318.
- Houser, J.N., P.J. Mulholland, and K.O. Maloney, 2005. Catchment disturbance and stream metabolism: patterns in ecosystem respiration and gross primary production along a gradient of upland soil and vegetation disturbance. *Journal of the North American Benthological Society* 24:538-552.
- Hynes, H.B.N., 1975. The stream and its valley. *Verhandlungen der Internationale Vereinigung für theoretische und angewandte Limnologie* 19:1-15.
- Izagirre, O., U. Agirre, M. Bermejo, J. Pozo, and A. Elosegi, 2008. Environmental controls of whole-stream metabolism identified from continuous monitoring of Basque streams. *Journal of the North American Benthological Society* 27:252-268.
- Kautsky, L., 1982. Primary production and uptake kinetics of ammonium and phosphate by *Enteromorpha compressa* in an ammonium sulfate industry outlet area. *Aquatic Botany* 12:23-40.
- Kemp, M.J., and W.K. Dodds, 2001. Spatial and temporal patterns of nitrogen concentrations in pristine and agriculturally-influenced prairie streams. *Biogeochemistry* 53:125-141.

- Lewis, T., and L.R. Taylor, 1967. *Introduction to Experimental Ecology*. Academic Press, London: 401 pp.
- Marzolf, E.R., P.J. Mulholland, and A.D. Steinman, 1994. Improvements to the diurnal upstream-downstream dissolved oxygen change technique for determining whole-stream metabolism in small streams. *Canadian Journal of Fisheries and Aquatic Sciences* 51:1591-1599.
- Marzolf, E.R., P.J. Mulholland, and A.D. Steinman, 1998. Reply: improvements to the diurnal upstream-downstream dissolved oxygen change technique for determining whole-stream metabolism in small streams. *Canadian Journal of Fisheries and Aquatic Sciences* 55:1786-1787.
- Massy, W.F., 1965. Principal components regression in exploratory statistical research. *Journal of the American Statistical Association* 309:234-256.
- McGarigal, K., S. Cushman, and S. Stafford, 2000. *Multivariate Statistics for Wildlife and Ecology Research*. Springer, New York: 283 pp.
- McTammany, M.E., J.R. Webster, E.F. Benfield, and M.A. Neatrour, 2003. Longitudinal patterns of metabolism in a southern Appalachian river. *Journal of the North American Benthological Society* 22:359-370.
- McTammany, M.E., E.F. Benfield, and J.R. Webster, 2007. Recovery of stream ecosystem metabolism from historical agriculture. *Journal of the North American Benthological Society* 26:532-545.
- Meyer, J.L., and R.T. Edwards, 1990. Ecosystem metabolism and turnover of organic carbon along a blackwater river continuum. *Ecology* 71:668-677.
- Metzler, G.M., and L.A. Smock, 1990. Storage and dynamics of subsurface detritus in a sand-bottomed stream. *Canadian Journal of Fisheries and Aquatic Sciences* 47:588-594.
- Minshall, G.W., 1978. Autotrophy in stream ecosystems. *BioScience* 28:767 - 771.
- Minshall, G.W., R.C. Petersen, K.W. Cummins, T.L. Bott, J.R. Sedell, C.E. Cushing, and R.L. Vannote, 1983. Interbiome comparison of stream ecosystem dynamics. *Ecological Monographs* 53:1-25.
- Mulholland, P.J., C.S. Fellows, J.L. Tank, N.B. Grimm, J.R. Webster, S.K. Hamilton, E. Marti, L. Ashkenas, W.B. Bowden, W.K. Dodds, W.H. McDowell, M.J. Paul, and B.J. Peterson, 2001. Inter-biome comparison of factors controlling stream metabolism. *Freshwater Biology* 46:1503-1517.

- Naiman, R.J., J.M. Melillo, M.A. Lock, T.E. Ford, and S.R. Reice, 1987. Longitudinal patterns of ecosystem processes and community structure in a subarctic river continuum. *Ecology* 68:1139-1156.
- National Council for Air and Stream Improvement, Inc. (NCASI), 2001. Patterns and processes of variation in nitrogen and phosphorus concentrations in forested streams. Technical Bulletin No. 836. Research Triangle Park, NC: National Council for Air and Stream Improvement, Inc.
- Odum, H.T., 1956. Primary production in flowing waters. *Limnology and Oceanography* 1:103-117.
- Ortiz-Zayas, J.R., W.M. Lewis, Jr., J.F. Saunders, J.H. McCutchan, and F.N. Scantena, 2005. Metabolism of tropical rainforest stream. *Journal of the North American Benthological Society* 24:769-783.
- Peterson, C.G., 1996. Response of benthic algal communities to natural physical disturbance. In: Stevenson, R.J., M.L. Bothwell, and R.L. Lowe, (editors), *Algal Ecology: Freshwater Benthic Ecosystems*. Academic Press, Burlington, MA: 375-402.
- Rathbun, R.F., D.W. Stephens, D.J. Schultz, and D.Y. Tai, 1978. Laboratory studies of gas tracers for reaeration. *Journal of the Environmental Engineering Division*. 104:215-229.
- Roberts, B.J., P.J. Mulholland, and W.R. Hill, 2007. Multiple scales of temporal variability in ecosystem metabolism rates: results from 2 years of continuous monitoring in a forested headwater stream. *Ecosystems* 10:588-606.
- Rosemond, A.D., P.J. Mulholland, and J.W. Elwood, 1993. Top-down and bottom-up control of stream periphyton: effects of nutrients and herbivores. *Ecology* 74:1264-1280.
- SAS Institute Inc., 2011. SAS/STAT® 9.3 User's Guide. Cary, NC, SAS Institute Inc.
- Sinsabaugh, R.L., 1997. Large-scale trends for stream benthic respiration. *Journal of the North American Benthological Society* 16:119-122.
- Sponseller, R.A., and E.F. Benfield, 2001. Influences of land use on leaf breakdown in southern Appalachian headwater streams: a multiple-scale analysis. *Journal of the North American Benthological Society* 20:44-59.
- Sponseller, R.A., E.F. Benfield, and H.M. Valett, 2001. Relationships between land use, spatial scale and stream macroinvertebrate communities. *Freshwater Biology* 46:1409-1424.
- Stanley, E.H., and A.K. Ward, 1997. Inorganic nitrogen regimes in an Alabama wetland. *Journal of the North American Benthological Society* 16:820-832.

- Stofleth, J.M., F.D. Shields, and G.A. Fox, 2008. Hyporheic and total transient storage in small, sand-bed streams. *Hydrological Processes* 22:1885-1894.
- Strahler, A.N., 1957. Quantitative analysis of watershed geomorphology. *Transactions of the American Geophysical Union* 8:913-920.
- Stream Solute Workshop, 1990. Concepts and methods for assessing solute dynamics in stream ecosystems. *Journal of the North American Benthological Society* 9:95-119.
- Tamminen, T., 1982. Effects of ammonium effluents on planktonic primary production and decomposition in a coastal brackish water environment. II. Interrelations between abiotic and biotic components of the planktonic ecosystem. *Netherlands Journal of Sea Research* 15:349-361.
- Tank, J.L., E.J. Rosi-Marshall, N.A. Griffiths, S.A. Entekin, and M.L. Stephen, 2010. A review of allochthonous organic matter dynamics and metabolism in streams. *Journal of the North American Benthological Society* 29:118-146.
- Tsivoglou, E.C., and L.A. Neal, 1976. Tracer measurement of reaeration: III. predicting the reaeration capacity of inland streams. *Journal of the Water Pollution Control Federation* 48:2669-2689.
- Vanni M.J., W.H. Renwick, J.L. Headworth, J.D. Auch, and M.H. Schaus, 2001. Dissolved and particulate nutrient flux from three adjacent agricultural watersheds: a five-year study. *Biogeochemistry* 54:85-114.
- Uehlinger, U., 2000. Resistance and resilience of ecosystem metabolism in a flood-prone river system. *Freshwater Biology* 45:319-332.
- Uehlinger, U., 2006. Annual cycle and inter-annual variability of gross primary production and ecosystem respiration in a flood-prone river during a 15-year period. *Freshwater Biology* 51:938-950.
- Wallace, J.B., and A.C. Benke, 1984. Quantification of wood habitat in subtropical coastal plain streams. *Canadian Journal of Fisheries and Aquatic Sciences* 41:1643-1652.
- Webster, J.R., and J.L. Meyer, 1997. Organic matter budgets for stream: a synthesis. *Journal of the North American Benthological Society* 16:141-161.
- Webster, J.R., P.J. Mulholland, J.L. Tank, H.M. Valett, W.K. Dodds, B.J. Peterson, W.B. Bowden, C.N. Dahm, S. Findlay, S.V. Gregory, N.B. Grimm, S.K. Hamilton, S.L. Johnson, E. Marti, W.H. McDowell, J.L. Meyer, D.D. Morrall, S.A. Thomas, W.M. Wollheim, 2003. Factors affecting ammonium uptake in streams - an interbiome perspective. *Freshwater Biology* 48:1329-1352.

- Wiley, M.J., L.L. Osborne, and R.W. Larimore, 1990. Longitudinal structure of an agricultural prairie river system and its relationship to current stream ecosystem theory. *Canadian Journal of Fisheries and Aquatic Sciences* 47:373-384.
- Young, R.G., and A.D. Huryn, 1998. Comment: improvements to the diurnal upstream-downstream dissolved oxygen change technique for determining whole-stream metabolism in small streams. *Canadian Journal of Fisheries and Aquatic Sciences* 55:1784-1785.
- Young, R.G., and A.D. Huryn, 1999. Effects of land use on stream metabolism and organic matter turnover. *Ecological Applications* 9:1359-1376.
- Young, R.G., C.D. Matthaei, and C.R. Townsend, 2008. Organic matter breakdown and ecosystem metabolism: functional indicators for assessing river ecosystem health. *Journal of the North American Benthological Society* 27:605-625.

CHAPTER 4. EXTREME EVENTS AFFECT ECOSYSTEM METABOLISM IN A SANDY, COASTAL PLAIN STREAM OF LOUISIANA

Introduction

Ecosystem metabolism measurements, comprised of gross primary production (GPP) and ecosystem respiration (ER), provide important information on the sources and sinks of dissolved oxygen and carbon in aquatic settings (Bott, 2006). In stream ecosystems, oxygen can be introduced in the water column through photosynthesis by primary producers or by atmospheric exchange, the latter usually facilitated by surface water turbulence, particularly in riffle habitats. Photosynthesis in the stream also results in the accrual of autochthonous organic matter (OM), which in most systems is supplemented by allochthonous OM inputs from upstream sources, the riparian zone, or the floodplain (Tank et al., 2010). Streams can be classified as net autotrophic or net heterotrophic depending on the relative magnitude of autochthonous and allochthonous production, and studies of stream metabolism can determine whether internal or external sources of carbon are more important for energy flow in the system (Tank et al., 2010). Importantly, streams can exhibit temporal changes in autotrophy and heterotrophy depending on available sunlight, herbivory, available nutrients, and disturbances such as changes in discharge during storms or droughts, all of which can affect both primary producers and heterotrophic organisms (Young et al., 2008).

Although most of our knowledge concerning the correlates of stream metabolism comes from spatial snapshots over short time intervals (e.g., Bott et al., 1985; Mulholland et al., 2001; Bernot et al., 2010), several recent studies have yielded longer-term continuous analyses of stream respiration for periods exceeding 1 year (Uehlinger, 2000; Acuña et al., 2004; Uehlinger, 2006; Roberts et al., 2007; Izagirre et al., 2008). Izagirre et al. (2008) studied many streams in

northern Spain over 15 months that ranged in size, canopy cover, and anthropogenic influence (including nutrient, urban, and industrial pollution), and found that GPP was usually higher when canopies were open and nutrient levels were high, whereas ER was fueled by organic pollution. Uehlinger (2000, 2006) reported that high discharge events scoured the algae and heterotrophic biofilms from gravel beds of 6th- and 7th-order rivers, with decreases in GPP exceeding declines in ER, causing the rivers to become heterotrophic. Roberts et al. (2007) also found stream heterotrophy increased following rain events due to both a depression in GPP and that increased dissolved organic carbon inputs from the catchment and caused a spike in rates of ER, whereas Acuña et al. (2004) reported that increases in stream discharge flushed OM from the site and decreased ER. The above studies emphasize that high stream discharge events can significantly affect both GPP and ER, causing algal scouring, re-sorting of sediment, and burial of both algae and OM, as well as the uncovering and re-suspension of previously buried OM from the hyporheic zone, especially in sandy coastal plain streams (Metzler and Smock, 2000). Discharge peaks during storm events tend to reset the stream to earlier successional stages and clear out algal dieback or senescing forms (Fisher et al., 1982; Peterson, 1996), which may be important to the maintenance of stream productivity.

This study was designed to address four questions concerning metabolism in a 3rd order, nutrient-rich stream with relatively clear water and a relatively flashy hydrograph in the coastal plain of southeastern Louisiana: (1) How do gross primary production (GPP) and ecosystem respiration (ER) vary throughout the year? (2) What controls ecosystem metabolism? (3) How do high discharge events affect GPP and ER in a dynamic coastal plain stream? (4) How does the resistance and resilience of GPP and ER rates change over the course of the year after a high discharge? Prevailing weather patterns result in periodic high-discharge events in this

catchment, and the minimally stable, sand-dominated sediments in the stream and surrounding riparian zone result in frequent floodplain scouring of vegetation and an open canopy. There are very few continuous measurements of GPP and ER in a mid-order stream with little channel stability, and this study is an important step in understanding temporal patterns of ecosystem respiration in these highly dynamic coastal plain systems.

Methods and Materials

I studied stream metabolism in West Fork of Thompson Creek (WFT), a 3rd-order stream located in the Southern Rolling Hills ecoregion of the Mississippi Valley Loess Plains. Originating in southwestern Mississippi, WFT converges with Thompson Creek, which subsequently drains into the Mississippi River about 25 kilometers northwest of Baton Rouge, LA (Fig. 1). The study reach was located about 32 km north of St. Francisville, LA, and was characterized by low gradients and flow velocities, sand-dominated substrates, and relatively clear water (Felley, 1982; Daigle et al., 2006). The low gradient and nearly laminar flows result in very few riffles and little turbulence-driven aeration or atmospheric gas exchange. When the stream experiences heavy rainfall events, considerable stream bed alterations, downstream movement of accumulated woody debris, and scouring of the floodplain occurs. The algal assemblage is dominated by the filamentous green algae *Spirogyra* spp. on the stream edge where velocity is lowest, and various diatoms within and on top of the sandy substrates.

I chose a 90-meter reach about 200 meters upstream of a bridge access point to measure physical attributes of the stream and establish upstream and downstream stations for solute injections. From July 2007 to December 2009, a YSI 6600EDS-S datasonde (Yellow Springs, OH) was placed in the stream and set to record temperature, dissolved oxygen (DO; Clark sensor

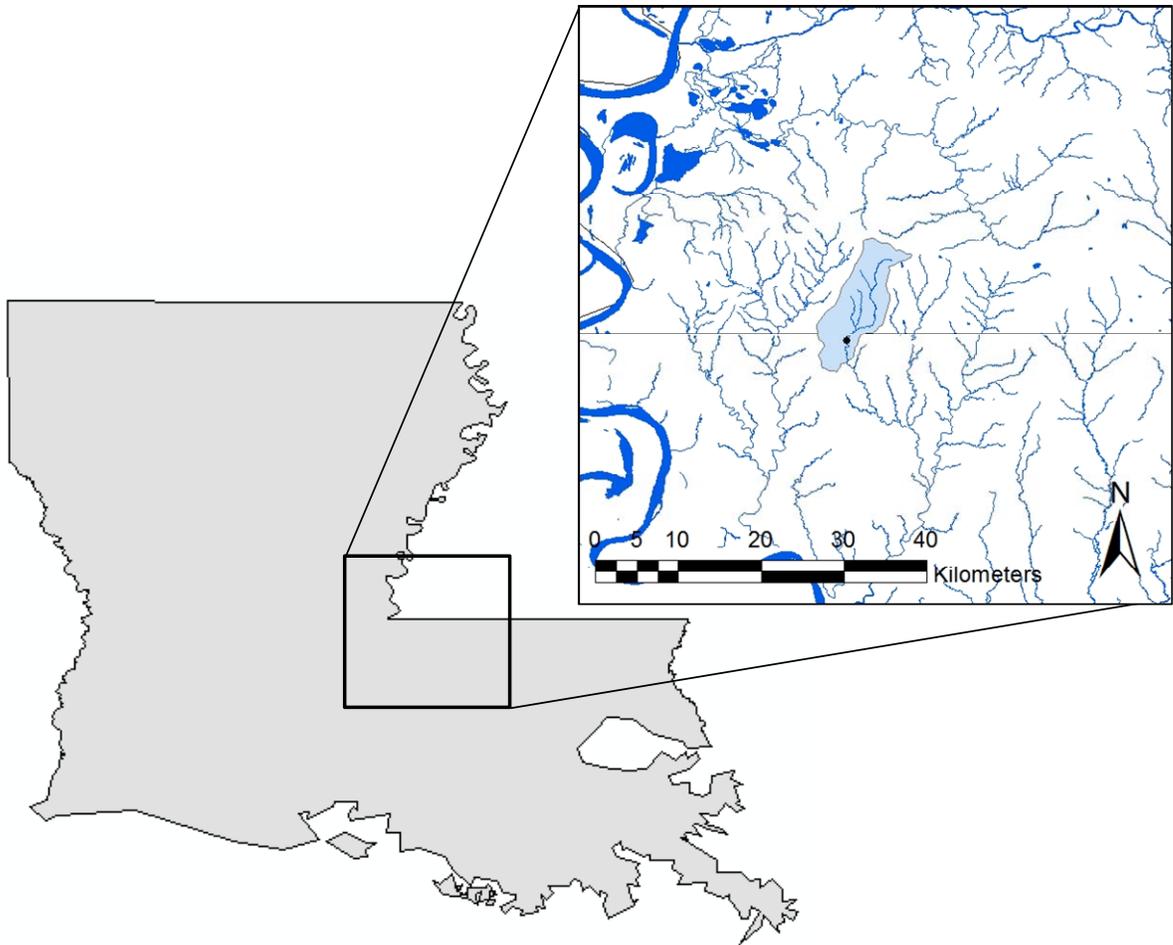


Fig. 1 Location of West Fork of Thompson and watershed upstream of the study reach.

probe), specific conductance, water depth, and pH every 15 minutes. Datasondes were replaced approximately every 2 weeks, with an overlap of at least 4 readings to assess variability among units and instrument drift. Calibration after retrieval was also used to aid in adjusting for instrument drift during the preceding 2 weeks. I calculated DO at saturation from water temperatures recorded during each 15-minute period (APHA, 2005). Wetted stream width was measured from transects placed every 10 m along the 90-m reach, and mean depth was estimated from 5 measurements along each transect (~10 cm from each bank and 25, 50, and 75% of

stream width). Stream stage was estimated as the surface water level above an arbitrary vertical datum located 1.5 m below a nail hammered into a streamside tree. Distance to water level was measured with a plumb ruler from the surface to the nail during YSI deployment and subtracted from 1.5 m to determine the instantaneous stream stage. That value was compared to the YSI depth reading and as the depth reading varied throughout deployment, stream stage was adjusted accordingly. Average, maximum, and minimum stream stage values were calculated for each day.

During 19 sampling trips from July 2009 to August 2011, I performed concurrent solute and propane injections to estimate stream velocity, stream discharge, and reaeration coefficients (Stream Solute Workshop, 1990; Bott, 2006). Solute injections involved a NaCl solution (conservative tracer) pumped into the stream about 40 – 50 m upstream with a Flojet 3000 series diaphragm pump model 03501503. Given the width of the stream, tubing was split into 5 evenly spaced outlets to facilitate even release of the solute across the stream and provide a shorter mixing distance as the injection traveled downstream. Each of the 5 outlets was adjusted with varying tubing sizes and/or clamps so that all discharges were within ~10% of one another. Two YSI 6820 V2 Multiparameter Water Quality sondes calibrated with the same calibration solution were used to measure specific conductance every 15 seconds at both upstream and downstream sites until readings stabilized at both stations. Average stream velocity was measured as the time of maximum rate of change in specific conductance (maximum slope of the change in the climbing limb of specific conductance) between the two stations, and stream discharge was calculated at each station as:

$$Q_i = \frac{Q_{pump} \times Cond_{inj}}{Cond_i - Cond_b} \quad (1)$$

where Q_i equals discharge at station i , Q_{pump} is the injection volume of the NaCl solution, and Cond_{inj} , Cond_i , and Cond_b are the specific conductance of the injection solution, the specific conductance at station i , and the stream's background specific conductance, respectively (Stream Solute Workshop, 1990; Bott, 2006).

Stream reaeration coefficients for oxygen (k_{O_2}) were estimated from propane injection and reaeration values. Similar to the solute injection, propane was bubbled into the stream through 5 cylindrical airstones (2.5 cm length x 1.3 cm diameter) placed longitudinally across the stream to ensure proper mixing. Five replicate water samples were collected from both the upstream and downstream stations after the NaCl solute injection had reached steady state conditions. For each sample, a 10-ml plastic syringe was rinsed several times with stream water, air bubbles were removed, and 6 ml was injected into 10-ml pre-evacuated vacutainers. Each vacutainer was air-equilibrated away from the stream and headspace gas was analyzed for propane concentration with a Shimadzu GC-2014 equipped with a Poropak 1/8-inch diameter, 6-foot length column (mesh 80/100) and a flame ionization detector at 150°C. Propane reaeration was calculated as:

$$K_{\text{propane}} = \frac{1}{\tau} \ln \left(\frac{G_u C_d}{G_d C_u} \right) \quad (2)$$

where τ is the travel time of water (min^{-1}) between the two stations, G_u and G_d are the propane concentrations of the upstream and downstream stations, respectively, and C_u and C_d are the conservative tracer concentrations at each station, corrected for background concentration (Marzolf et al., 1994). I calculated k_{O_2} from k_{propane} with the standard conversion $k_{\text{O}_2} = k_{\text{propane}} \times 1.39$ (Rathbun et al., 1978). Concurrent conservative solute and propane tracer study trips yielded discrete, stream velocity, discharge, stream depth, and stream width estimations. Stream

depth was converted to stream stage and regressions of these values with stream stage allowed for the interpolation of these variables during unattended YSI deployment.

Continuous estimates of daily GPP and ER were calculated from open-system, single-station diel DO curves (Bott 2006). The rate of change in DO concentration was calculated as the difference between consecutive 15-minute DO readings, and ecosystem metabolism was determined from the change in DO over this interval based on the equation:

$$\Delta DO = GPP - ER + k_{O_2}(C_s - C) \quad (3)$$

where ΔDO is the change in DO concentration ($\text{g O}_2 \text{ m}^{-3}$), GPP and ER are volumetric gross primary production and ecosystem respiration ($\text{g O}_2 \text{ m}^{-3}$) between consecutive 15-minute DO measurements, and $(C_s - C)$ represents the deficit or saturation of O_2 in the system, i.e., C_s is the saturation concentration of O_2 at the measured water temperature (calculated according to APHA, 2005), and C is the actual concentration. When C_s is greater than C , this term represents a net deficit and O_2 diffuses into the stream and vice versa. By multiplying the deficit/saturation by k_{O_2} , the reaeration coefficient, the 3rd member in the equation represents the net exchange of O_2 with the atmosphere over the measurement interval. These values are multiplied by the calculated stream depth from the mean stream depth-stream stage relationship to provide areal estimates of GPP and ER ($\text{g O}_2 \text{ m}^{-2}$). During the night, GPP is 0, thus:

$$ER = \Delta DO - k_{O_2}(C_s - C). \quad (4)$$

During daylight hours, ER is extrapolated from nighttime estimates to the full 24-hour period, with integration of GPP values to determine daily values of both ER and GPP ($\text{g O}_2 \text{ m}^{-2} \text{ day}^{-1}$). In these calculations, ER values are negative as they represent a net loss of O_2 from the system. Net ecosystem production (NEP) is the sum of GPP and ER.

Photosynthetically Active Radiation (PAR) was measured with an Onset S-LIA-M003 PAR sensor and H21-002 HOBO Micro Station Data Logger from March 2010 to late May 2010 when the unit was damaged, presumably by a flood. Instantaneous PAR was measured every 1 minute, averaged and recorded by the data logger every 15 min. Daily PAR rates were determined by integrating the 15-minute readings for each day. These values were compared to solar radiation data reported by the LSU Ag Center research stations (available at: <http://weather.lsuagcenter.com/>) in order to determine the best station to use for light data during datasonde deployment. I choose radiation data from the LIGO corner research station in Livingston, Louisiana, with solar radiation data converted PAR according to McCree (1971). Of all the nearest stations, LIGO station had the best fit with our PAR sensor over the approximately three months the HOBO was active ($n=111$, $R^2 = 0.3717$, $p < 0.01$).

Resistance was measured as the minimum stage change that resulted in a visual depression of GPP and was converted to stream velocity via the stage-velocity regression. Resilience of GPP was calculated as the approximate number of days post-storm during which GPP returned to at least 50% of the pre-storm levels. Resilience was regressed against the increase in stream stage (i.e., storm surge) to determine resiliency slopes for the winter rainy season (November through mid-April), and the summer dry season (late-April through late October). All regressions and comparisons of model coefficients (i.e., regression slopes) for resilience for each season were carried out in SAS 9.3 (SAS 2011).

Results

Mean stream depth, stream velocity, stream discharge, and reaeration all exhibited positive relationships with stream stage (Fig. 2), with stage explaining 44%, 52%, 58%, and

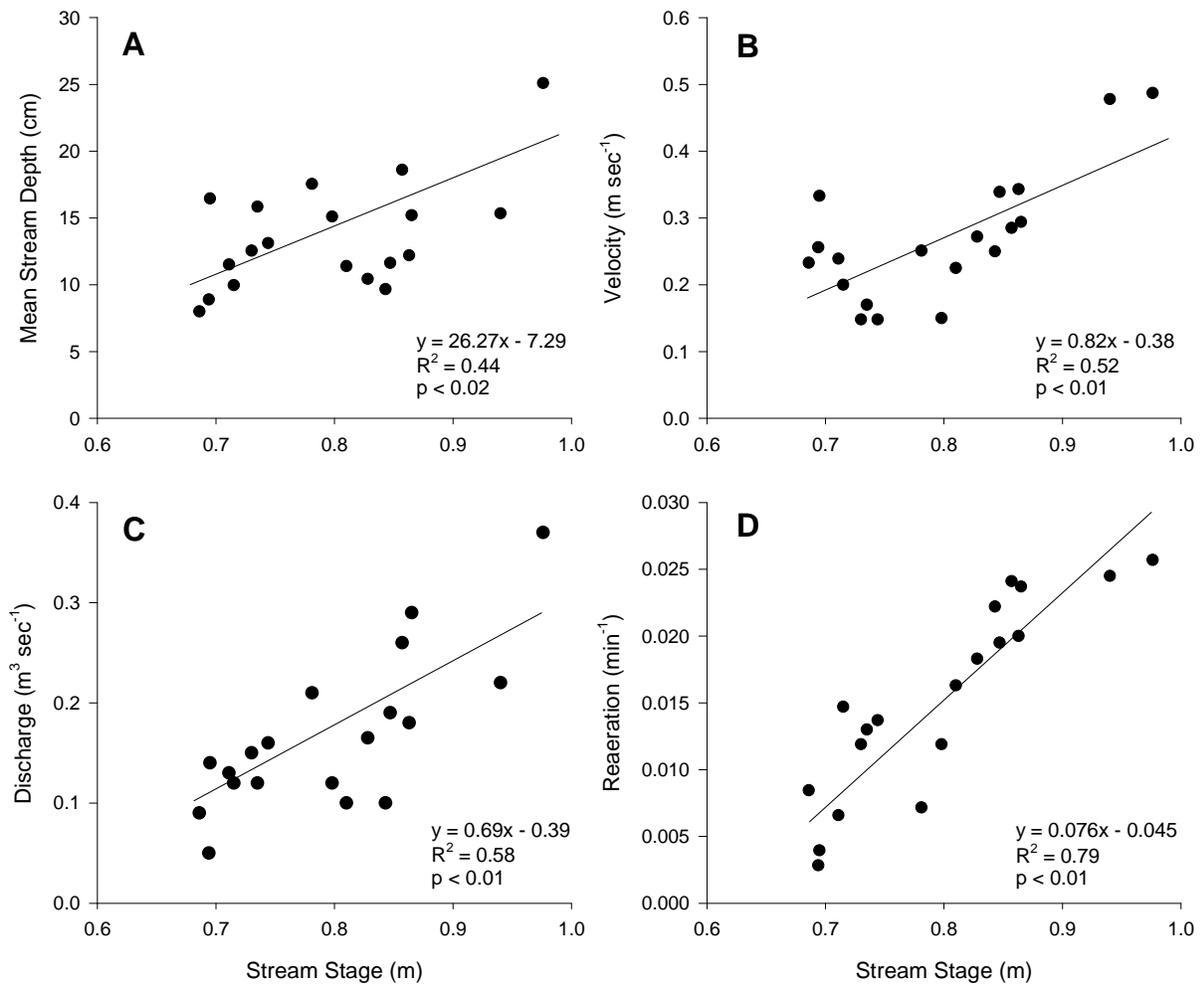


Fig. 2 Stream stage varies linearly with measurements of (A) mean stream depth, (B) stream velocity, (C) stream discharge, and (D) oxygen reaeration calculated from solute-propane injections ($n = 19$).

79%, respectively, of the range of each parameter. I used the stage- k_{O_2} relationship to continuously estimate GPP and ER for WFT, but limited my estimates to stream stages between 0.68 and 1.0 because: 1) safety issues prevented discharge and reaeration measurements at elevated stream stages during storm events; 2) conspicuous depressions in DO levels were evident during rising stream stages (see also Uehlinger, 2000); 3) the datasonde was often buried

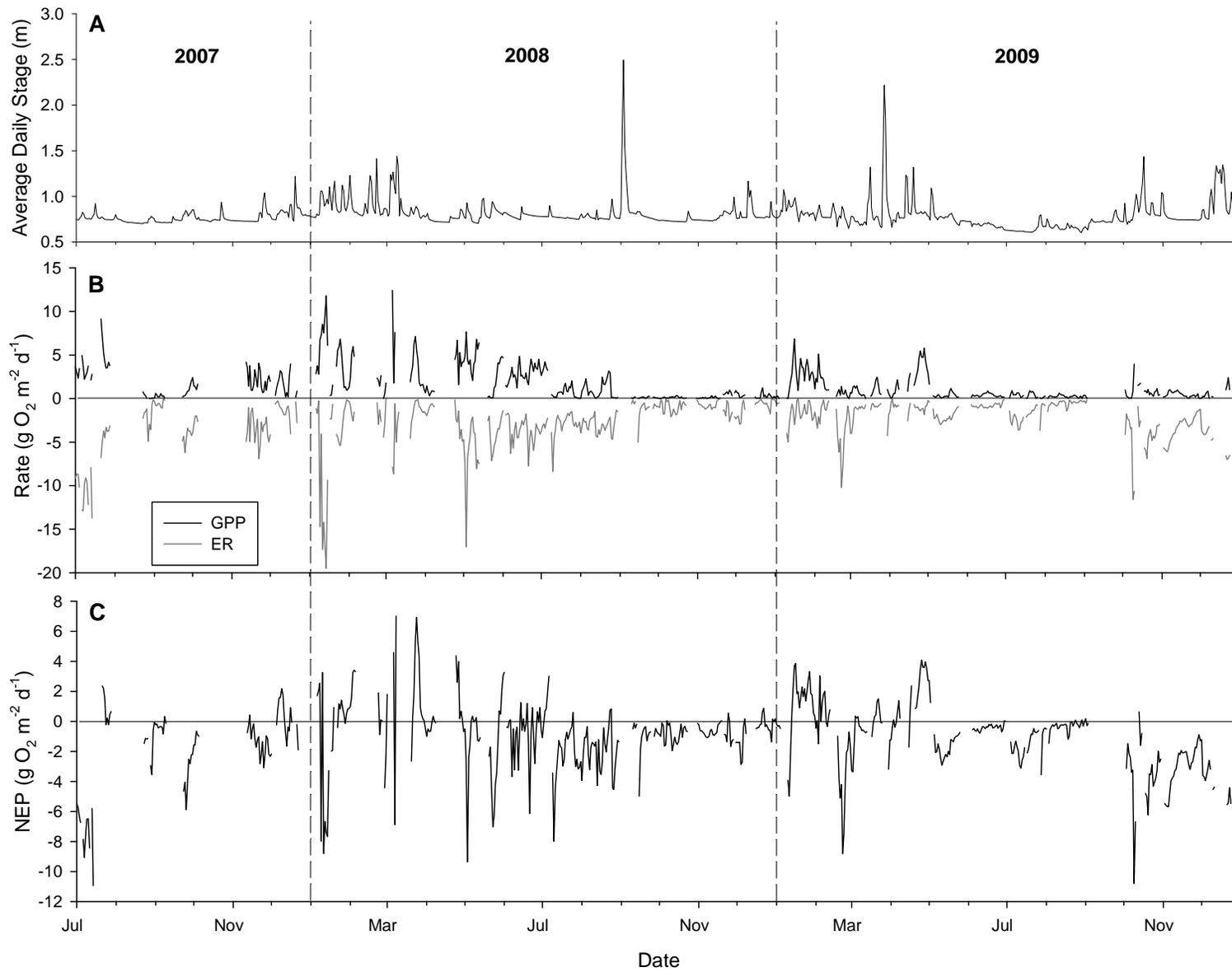
during storm events by the shifting stream bed; and 4) the stage- k_{O_2} relationship may not have been linear above and below my measured data range (Izagirre et al. 2000). From July 1, 2007 – December 24, 2009, ecosystem metabolism was calculated on 631 of the 908 possible days, or 69%.

Stream stage was averaged each day, and any missing values (e.g., buried datasonde) were estimated from a stage-stage regression with a nearby USGS stream gauging station (USGS 07377500 Comite River near Olive Branch, LA; $R^2 = 0.52$, $n=111$). Although the period from November through April tended to have a higher frequency of storms, mean stream stage was highly variable throughout the study period. Two large rain events resulted in mean daily stream stages over 2 m, including rainfall associated with the landfall of Hurricane Gustav in early September 2008 (Fig. 3A).

Rates of GPP and ER in WFT ranged from $<0.01 - 12.43 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ and $<0.01 - 19.49 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$, respectively, and varied considerably throughout the study period (Fig. 3B). Temporal patterns of NEP indicated dynamic switching between net autotrophy and net heterotrophy in WFT (Fig. 3C). Overall, the stream appeared to maintain mostly net heterotrophic conditions during much of each year, especially during fall and early winter. Interestingly, data indicated a general increase in GPP during the beginning of both years when stream temperatures and daily PAR (Fig. 4) were at their lowest levels. GPP in WFT was not correlated with PAR ($r = 0.03$) over the two-year study.

Spates usually resulted in a decrease in GPP and a subsequent increase in ER, whereas stable flow periods resulted in increases in GPP in summer 2008 and a depression in summer 2009. In summer months, storms and subsequent increases in stream stage resulted in a depression of GPP and stimulation of ER, which gradually returned to pre-storm conditions as

Fig. 3 (on the following page). Daily mean stream stage (A) and rates of gross primary production (GPP) and ecosystem respiration (ER; B) are highly variable throughout the study period. Net ecosystem production (NEP; C) was also highly variable throughout the study period with possible dynamic switching between autotrophy and heterotrophy after storms. Positive values of NEP represent when the stream is net autotrophic while negative values indicate net heterotrophy.



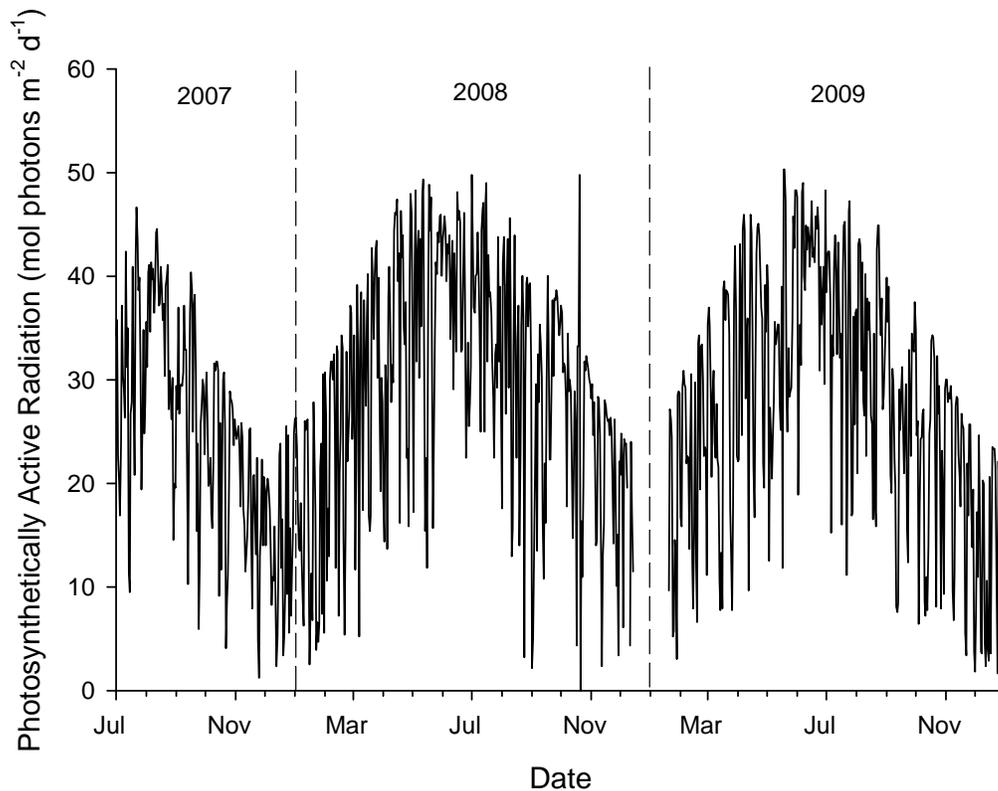


Fig. 4 Photosynthetically active radiation (PAR) varied throughout the study period with maxima in summer months and minima in winter. PAR was taken from LIGO corner research station in Livingston, Louisiana, with solar radiation data converted PAR according to McCree (1971).

time passed (Fig. 5A, C). However, storm effects on GPP or ER during the winter months were not as pronounced (Fig. 5B, D), and on a few occasions, spates actually stimulated GPP (Fig. 6). From June to early July 2008, fairly stable stream flows allowed noticeable patches of filamentous *Spirogyra* spp. to spread across the channel instead of being limited to the stream edges, which resulted in high GPP and ER rates. In contrast, both GPP and ER were relatively lower during the same period in 2009 when even more lower baseflow conditions occurred, particularly in late summer (Fig. 7). In addition to these seasonal and annual differences, patterns of change in GPP and ER were significantly different after the two large storm events.

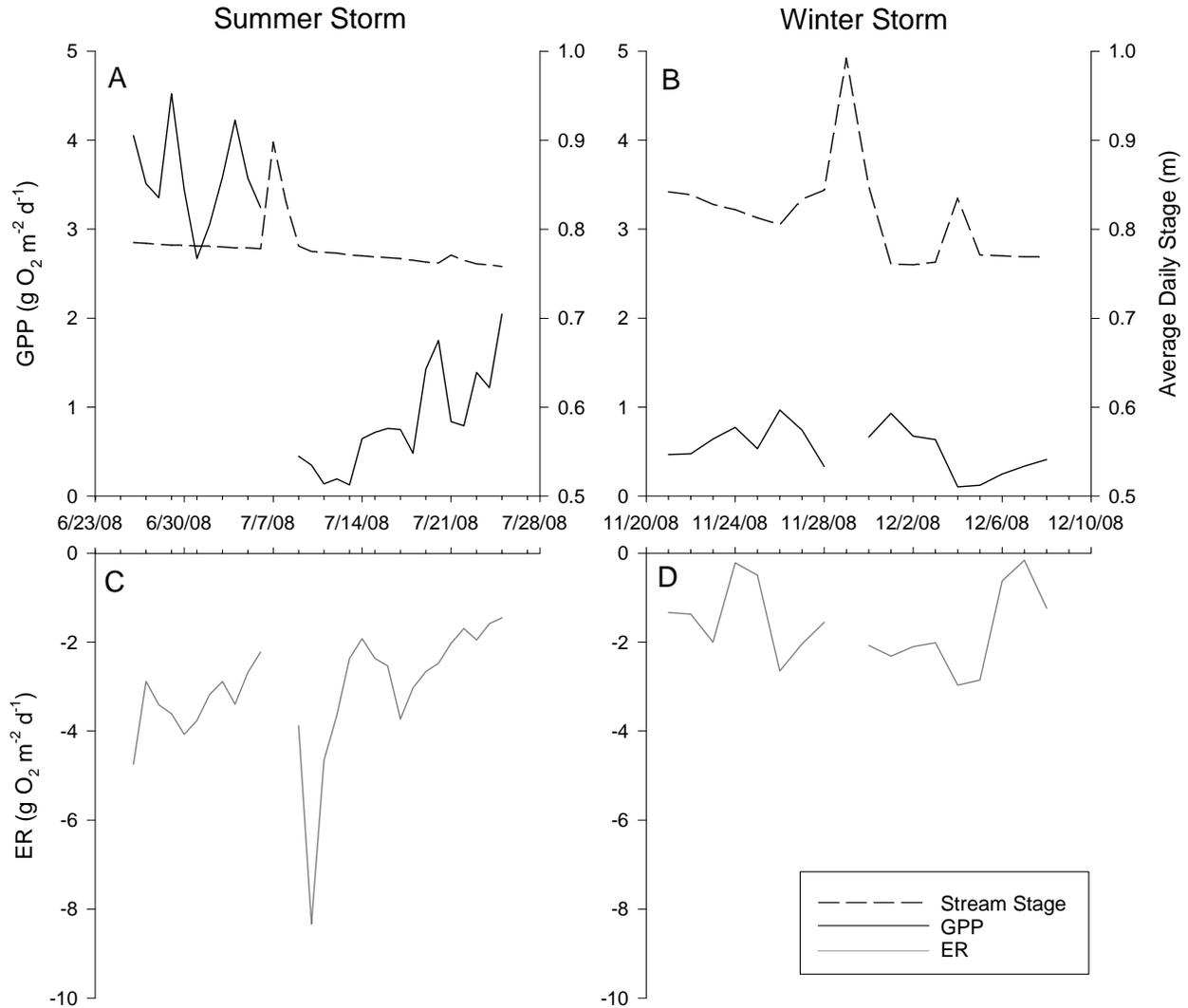


Fig. 5 Typical summer and winter storms and the resulting effects on mean daily stream stage (A, B), gross primary production (GPP), and ecosystem respiration (ER; C, D). Ecosystem metabolism data during larger storms are not reported as dissolved oxygen is depressed during increased discharge affecting GPP and ER calculations.

Whereas both GPP and ER were depressed (low NEP) during a long period of baseflow after the passage of Hurricane Gustav, both GPP and ER returned to pre-storm levels relatively quickly after passage of the large storm in late March 2009 that was followed by several smaller spates.

Using the approximate minimum value of stage that resulted in a depression of GPP and the stage-velocity regression, velocities above 0.356 m sec⁻¹ appeared to be the minimum

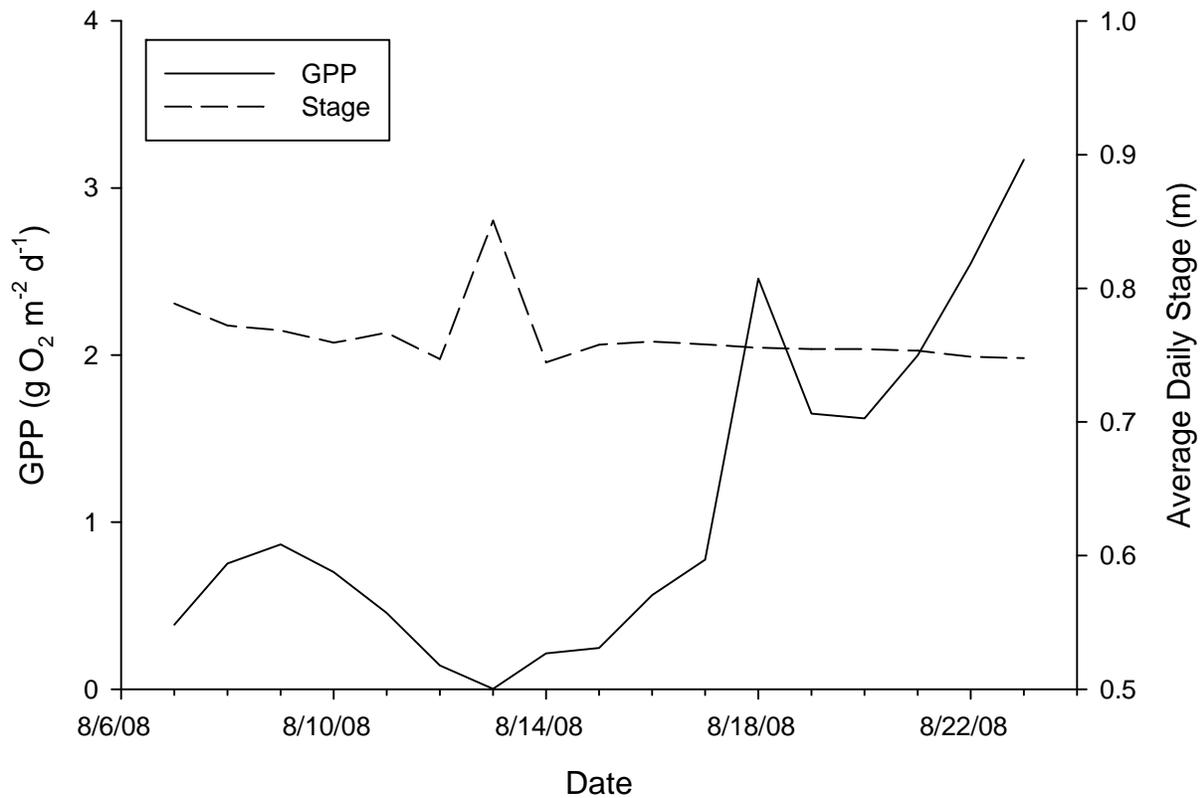


Fig. 6 One of example of when a storm caused a stimulus in gross primary production (GPP) in mid-August, 2008.

velocity of GPP resistance. However, I did not observe any sediment movement during the two sampling trips when velocity only slightly exceeded this level, so this flow level appeared to affect only algal processes while larger velocities can affect both algae and sediments.

Resilience, as measured via recovery time, was significantly different between winter and summer seasons (Fig. 8). Post-spate rates of recovery occurred much faster in winter than summer, even with large surges in stage.

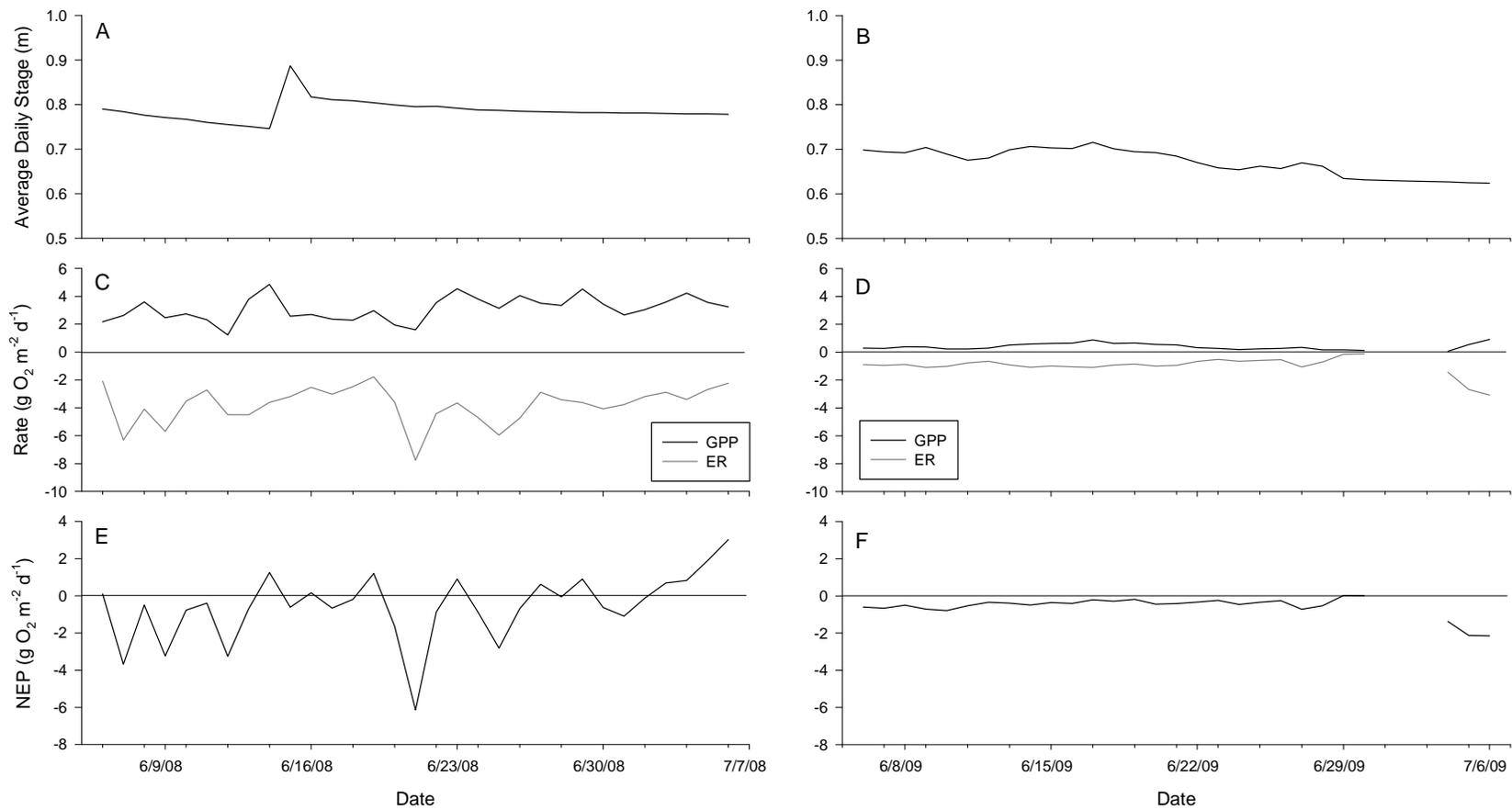


Fig. 7 Average daily stage (A,B), rates of gross primary production (GPP) and ecosystem respiration (ER; C,D), and net ecosystem production (NEP; E,F) from June – early July in 2008 and 2009, respectively, showed different patterns in ecosystem metabolism.

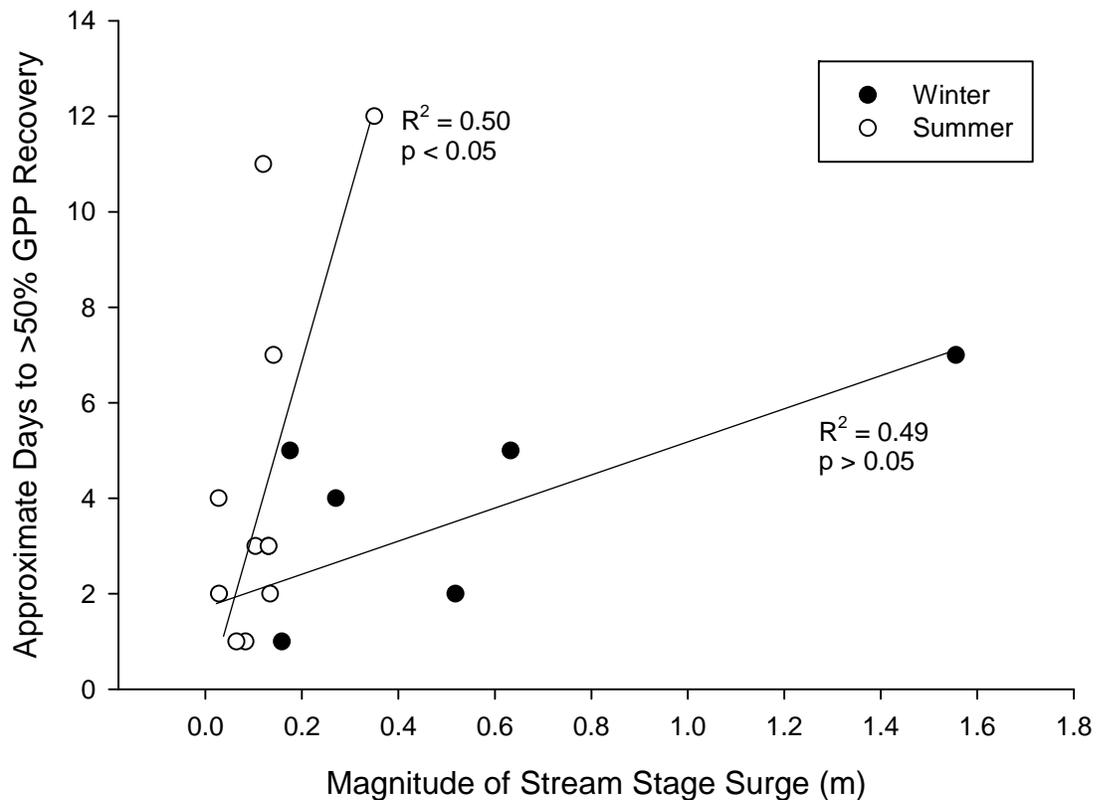


Fig. 8 Recovery of pre-storm gross primary production (GPP) rates to at least 50% pre-storm conditions depended on the magnitude of the storm. Resilience of algal communities differ between seasons as the slopes of the regression lines by season was significantly different ($t = 2.96$; $df = 1$; $p = 0.01$).

Discussion

Similar to other coastal plain or lowland streams, substrates in WFT are dominated by sand, which is readily moved during periods of increased discharge associated with storm passage (Felley, 1992). In addition to the scour and deposition of bed materials, storms can also affect stream morphology through lateral movement of the channel within its floodplain, as well as removal and deposition of vegetation, leaves, or LWD from both the stream proper and the

riparian zone. Sediment movement can affect ecosystem processes such as GPP by scouring or burying algae (Fisher et al., 1982; O'Connor and Lake, 1994; Peterson, 2006), as well as ER through the redistribution, burial, or re-suspension of previously buried OM (Metzler and Smock, 2000; Acuña et al, 2004). In the benthically unstable WFT, I found GPP was not only depressed after passage of a storm, but the period of GPP recovery was related to both storm magnitude and time of year. Additionally, ER was either stimulated and depressed by storms, again depending on the magnitude and timing of the spate.

Movement of bed materials in WFT during high discharge events affected the precision of the relationships between stream stage and depth or discharge. During periods of relatively stable flow, stream morphology changed little and depth or discharge varied predictably with small increases or decreases in stream stage, similar to streams with coarser, more stable substrates. However, stream morphology changed with each passing storm, and hydrologic variables followed suit. For example, two of the three highest velocities and discharges (Fig. 2B and 2C) were recorded during consecutive weekly trips after a bed-moving spate in June 2011, but occurred during moderate stages. In WFT, floods commonly reconfigured the position of pools, runs, and riffles, which appeared to alter the relationships between stream stage and depth or discharge with each subsequent storm. The dynamic nature of the WFT environment was obvious throughout the study, as I observed the stream move several meters from one side of the channel to the other and back on 3 consecutive weeks of high storm activity during February 2008. This lateral and longitudinal movement of the channel with discharge events is common in the migration zone of sandy lowland or low gradient streams (Felley, 1982; Metzler and Smock, 1990; Naiman et al., 2000). Moreover, these conditions can be highly problematic with

continuous ecosystem metabolism measurements, especially if the relationships with depth, discharge, velocity, and reaeration change with each spate.

Storm-related effects on stream algal biomass and GPP have been reported in several studies in recent decades (e.g., Fisher et al., 1982; Peterson, 1996; Uehlinger, 2000), with significantly greater impacts reported from lowland stream systems with sand-dominated substrates (Biggs et al., 1999a). Most of these disturbances do not completely remove algae from a stream, but instead leave behind small, heterogeneous algal patches due either to their location in the stream (e.g., along the edges or behind large, stable objects such as logs or boulders) or their morphology (e.g., low-profile or adnate taxa), which allows for recovery of the algal assemblage to pre-disturbance conditions (Peterson, 1996). The size and duration of the storm is particularly important, as extremely large flood events can scour the stream of almost all algae, regardless of sediment size or stability or the characteristics of the algal community (Peterson, 1996). Recolonization of scoured substrata can be rapid due to immigrating propagules, especially under conditions that favor the growth of diatoms (Fisher et al., 1982). However, there is evidence that very large floods can deplete the stream of its algal immigration pool and slow recolonization times (Stevenson, 1990; Uehlinger, 1991). The floodpulse after Hurricane Gustav was particularly detrimental to primary production, as the sheer magnitude of the storm appeared to remove much of the algae including potential propagules from the system, which resulted in a long recovery period.

In addition to storm intensity, flood-related losses of algal biomass also depend on the propensity for mobilization of benthic substrata. The tumbling, abrasive effect of sand lifted into solution can damage algae not recessed within substrate crevices and scour algal cells from exposed surfaces (see review by Peterson, 1996). Burial of algae reduces light availability, but

some algae have adapted to epipsammic or epipellic lifestyles and are able to either endure long periods of time buried in anoxic environments or are motile and can move back onto the surface (Moss 1977). Algae in WFT were predominately either filamentous *Spiragya* spp. or an assemblage of numerous species of diatoms loosely associated with the sediment, and post-storm depressions in GPP suggested that the algal assemblage as a whole was severely impacted by bed movements during periods of elevated discharge.

The amount of time between disturbances is also an important factor influencing stream GPP, particularly in fine-substrate streams. If the time interval is typically short, then the algal assemblage is dominated by smaller profile or non-filamentous taxa that are more resistant to scour and the effects of flooding, whereas long, filamentous or larger profile algae are much more prevalent in the algal assemblage as time intervals between storms increase (Peterson, 1996). Therefore, algal movement and mortality and the consequent effects on GPP caused by storms is a function of both size of the flood and the time since the last disturbance (Peterson, 1996). However, if the time interval between storms is sufficiently long, other factors such as growth space, light availability (shading of algae in the deeper layers), and nutrients become important, and can reduce GPP through algal senescence and sloughing (Uehlinger, 2006; Izagirre et al., 2007). In many studies, GPP has been correlated with chlorophyll *a*, alone or as part of multiple regression models (e.g., Bott et al., 1985; Acuña et al., 2004; Bott et al., 2006; Roberts et al., 2007), especially in streams with high nutrients (McTammany et al., 2007). However, there are several studies where chlorophyll *a* was not correlated with GPP (Mulholland et al., 2001), especially when factors such as sediment instability (Uehlinger and Naegeli, 1998; Atkinson et al., 2008), herbivory (Ortiz-Zayas et al., 2005), or prolonged growth periods were present (Izagirre et al., 2007). Thus, GPP may be higher in newly established or rapidly growing

algal assemblages when density dependent factors are not important, or when sediments are fairly stable, but low in areas of increased instability or prolonged growth. In this scenario, storms could serve to re-set the system (particularly after a long period of stable flows) and actually increase subsequent GPP during the growth phase of the algal assemblage when new areas are available for colonization or limitations such as low nutrients are relaxed (Peterson, 1996). Stable flow conditions in WFT during summer may have permitted growth of the algal community to a point where density dependent factors limited GPP. In fact, GPP actually increased after the passage of a few summer storms, which may have been related to the flushing of accumulated dead or senescing algae from the study reach, and the establishment of new space for recolonization. When disturbance levels were intermediate, i.e., relatively frequent mid-size storms, GPP seemed to recover quicker and rates tended to be higher than during long periods of stable flow or after passage of large storms.

Storm-related increases in discharge can also affect stream ER via input, export, or redistribution of OM that fuels heterotrophic respiration. Storms can input OM from the catchment or adjacent riparian and floodplain areas and stimulate ER (Meyer and Edwards, 1990; Roberts et al., 2007), but can also depress ER through the removal of loose detritus or leaf litter from the stream (Biggs et al., 1999b; Acuña et al., 2004; Acuña et al., 2007). In sandy or alluvial streams with unstable sediments, floods can negatively and positively affect ER, either because of the redistribution of OM through burial into the hyporheic zones where respiration may occur at slower rates, or through the uncovering or re-suspension of previously buried OM (Metzler and Smock, 1990). The magnitude of flooding may also be important in determining the overall effects on ER; for example, Gerull et al. (2012) found that sediment disturbance at greater sediment depths stimulated ER in experimental streams. In addition to physical

disturbance effects on ER, the biotic characteristics of sand-dominated systems may also play a significant role in the observed ER patterns. In general, OM decomposition and ER occurs at slower rates in unstable substrata due to the low numbers of invertebrate shredders that can tolerate sand substrates, as some invertebrates have been associated with increased decomposition rates of allochthonous OM such as leaf input (Rounick and Winterbourn, 1983). For the majority of storms that impacted WFT, ER was stimulated after floods, including a brief increase after the extremely high rainfall following Hurricane Gustav, although this increase was followed by prolonged depression within a few days. I believe that the decline in ER during this period (which lasted through fall and early winter) was due to the loss of much of the OM inventory in the system from the extremely high discharges associated with the hurricane (JLW, personal observation).

Although NEP rates in WFT tended to oscillate between net autotrophic and heterotrophic states, the stream was net heterotrophic for much of the year, suggesting that most of the energy came from allochthonous sources. Floods caused the stream to become either more net heterotrophic or drove the stream from a net autotrophic to a net heterotrophic state. Previous studies have shown a similar trend of floods affecting both GPP and ER, usually by causing a reduction in GPP and either a slight decrease or even an increase in ER (Uehlinger, 2000; Uehlinger, 2006; Roberts et al., 2007). However, Acuña et al. (2004, 2007) reported enhanced GPP in a closed canopy 3rd-order stream in Spain during wetter years because of less accumulated BOM and lower OM residence times and hence less detritus covering the substrate. Recovery time after flooding appears to vary by stream and season. For example, GPP recovery times after storms were shorter in summer when light availability was higher, while ER recovery lacked any seasonal pattern (Uehlinger, 2006). In contrast, GPP and ER resilience after

disturbance in a 3rd order stream in Spain were mediated by light in the spring, prior to canopy closure, and OM input in autumn (Acuña et al., 2007). WFT tended to behave like these streams where storms caused depression in GPP similar to the gravel streams studied by Uehlinger (2000; 2006) but where ER was rarely depressed after passage of a storm, regardless of season. However, GPP recovery in WFT was much faster in winter and spring, similar to the studies of Acuña et al. (2007). I did not assess recovery after Hurricane Gustav because GPP recovery was not evident for several months.

My measured reaeration rates using propane evasion are similar to those reported in Bott et al. (2006), but were low relative to other studies in a diversity of stream types (Mulholland et al., 2001; Acuña et al., 2004; Houser et al., 2005; Roberts et al., 2007). I expected k_{O_2} to be low because streamflow in WFT was nearly laminar, with few riffles or instream flow obstructions such as logs to cause turbulence or water mixing and entrainment or release of gas with the atmosphere. A linear relationship was apparent with stream stage and reaeration within the range of stages that I was able to access the stream. Increases in reaeration with rising stream discharge has been reported in past studies with propane evasion (Roberts et al., 2007) and nighttime regression calculations of k_{O_2} (Izagirre et al., 2007), although in the latter, some of the relationships were non-linear. In WFT, stream stage was significantly correlated with discharge, but it is possible that the relationship between stage and k_{O_2} may be non-linear. A straight line through the data would result in negative values at low stage (i.e., <0.6 m). Although Izagirre et al. (2007) found that the logarithm of reaeration either increased or decreased linearly with discharge, I believe that the actual relationship in WFT may be sigmoidal, slowly approaching zero at low depths with an asymptote at higher stages. The low reaeration potential of this stream indicates that catastrophic events such as sewage leaks could result in serious and

prolonged impacts on DO levels in the stream. Most organisms can recover from short periods of hypoxic or anoxia, but a prolonged period of low oxygen with slow reaeration could result in extensive fish or invertebrate kills in WFT.

Seasonality of GPP and ER rates was apparent in WFT, with higher rates of GPP in spring and summer likely due to warmer temperatures, increased sunlight, and longer photoperiods. However, there were exceptions to this trend that may have been related to the dominance of sand substrates in the stream. Atkinson et al. (2008) reported that constantly moving sediments depressed GPP rates in a clear, nutrient-rich stream throughout the year in Australia. In summer 2008 (higher discharge), rates of GPP were high in summer but depressed after Hurricane Gustav. However, GPP was also depressed in summer 2009 (lower discharge), which may have been related to a lack of sufficiently high flows to clear away senescing algae, as well as herbivory by macroinvertebrates (Ortiz-Zayas et al., 2005) or shading caused by overlying detritus (Acuña et al., 2007). Overall, large storms or long periods of stable flow had significant impacts on GPP and ER in this coastal plain stream, with effects mediated by the interaction of stream discharge and substrate stability. Lowland coastal streams represent dynamic systems where stochastic environmental conditions interact with the predictability of annual or seasonal patterns in GPP and ER. This study suggests that an intermediate disturbance regime, both in storm frequency and magnitude, may be most conducive to maintaining the highest stream metabolism rates in sand-dominated coastal streams.

References

Acuña, V., A. Giogi, I. Munoz, U. Uehlinger, and S. Sabater, 2004. Flow extremes and benthic organic matter shape the metabolism of a headwater Mediterranean stream. *Freshwater Biology* 49:960-971.

- Acuña, V., A. Giorgi, I. Muñoz, F. Sabater, and S. Sabater, 2007. Meteorological and riparian influences on organic matter dynamics in a forested Mediterranean stream. *Journal of the North American Benthological Society* 26:54-69.
- APHA (American Public Health Association), 2005. *Standard Methods for the Examination of Water and Wastewater*. 20th edition. American Public Health Association. Washington, DC.
- Atkinson, B.L., M.R. Grace, B.T. Hart, and K.E.N. Vanderkruk, 2008. Sediment instability affects the rate and location of primary production and respiration in a sand-bed stream. *Journal of the North American Benthological Society* 27:581-592.
- Bernot, M.J., D.J. Sobota, R.O. Hall, P.J. Mulholland, W.K. Dodds, J.R. Webster, J.L. Tank, L.R. Ashkenas, L.W. Cooper, C.N. Dahm, S. Findlay, S.V. Gregory, N.B. Grimm, S.K. Hamilton, S.L. Johnson, W.H. McDowell, J.L. Meyer, B.J. Peterson, G.C. Poole, H.M. Valett, C. Arango, J.J. Beaulieu, A.J. Burgin, C. Crenshaw, A.M. Helton, L. Johnson, J. Merriam, B.R. Niederlehner, J.M. O'Brien, J.D. Potter, R.W. Sheibley, S.M. Thomas, and K. Wilson, 2010. Inter-regional comparison of land-use effects on stream metabolism. *Freshwater Biology* 55:1874-1890.
- Biggs, B.J.F., R.A. Smith, and M.J. Duncan, 1999a. Velocity and sediment disturbance of periphyton in headwater streams: biomass and metabolism. *Journal of the North American Benthological Society* 18:222-241.
- Biggs, B.J.F., N.C. Tuchman, R.L. Lowe, and R.J. Stevenson, 1999b. Resource stress alters hydrological disturbance effects in a stream periphyton community. *Oikos* 85:95-108.
- Bott, T.L., 2006. Primary production and community respiration. In: Hauer, F.R., and G.A. Lamberti, (editors), *Methods in Stream Ecology*, 2nd edition. Academic Press, Burlington, MA: 663-690.
- Bott, T.L., J.T. Brock, C.S. Dunn, R.F. Naiman, R.W. Ovink, and R.C. Petersen, 1985. Benthic community metabolism in four temperate stream systems: an inter-biome comparison and evaluation of the river continuum concept. *Hydrobiologia* 123:3-45.
- Felley, J.D., 1992. Medium-low-gradient streams of the Gulf Coastal Plain. In: Hackney, C.T., S.M. Adams, and W.H. Martin (editors). *Biodiversity of the Southeastern United States: Aquatic Communities*. John Wiley and Sons, New York: 233-269.
- Fisher, S.G., L.J. Gray, N.B. Grimm, and D.E. Busch, 1982. Temporal succession in a desert stream ecosystem following flash flooding. *Ecological Monographs* 52:93-110.
- Flecker, A.S., B.W. Taylor, E.S. Bernardt, J.M. Hood, W.K. Cornwell, S.R. Cassatt, M.J. Vanni, and N.S. Altman, 2002. Interactions between herbivorous fishes and limiting nutrients in a tropical stream ecosystem. *Ecology* 83:1831-1844.

- Daigle, J.J., G.E. Griffith, J.M. Omernik, P.L. Faulker, R.P. McCulloh, L.R. Handley, L.M. Smith, and S.S. Chapman, 2006. Ecoregions of Louisiana (Color poster with map, descriptive text, summary tables, and photographs). Reston, Virginia. U.S. Geological Survey.
- Hall, R.O., and J.L. Tank, 2003. Ecosystem metabolism controls nitrogen uptake in streams in Grand Teton National Park, Wyoming. *Limnology and Oceanography* 48:1120-1128.
- Hill, W.R., H.L. Boston, A.D. Steinman, 1992. Grazers and nutrients simultaneously limit lotic primary productivity. *Canadian Journal of Fisheries and Aquatic Sciences* 49:504-512.
- Izagirre, O., U. Agirre, M. Bermejo, J. Pozo, and A. Elosegi, 2008. Environmental controls of whole-stream metabolism identified from continuous monitoring of Basque streams. *Journal of the North American Benthological Society* 27:252-268.
- Marzolf, E.R., P.J. Mulholland, and A.D. Steinman, 1994. Improvements to the diurnal upstream-downstream dissolved oxygen change technique for determining whole-stream metabolism in small streams. *Canadian Journal of Fisheries and Aquatic Sciences* 51:1591-1599.
- McCree, K.J., 1972. Test of current definitions of photosynthetically active radiation against leaf photosynthesis data. *Agricultural Meteorology* 10:443-453.
- McTammany, M.E., E.F. Benfield, and J.R. Webster, 2007. Recovery of stream ecosystem metabolism from historical agriculture. *Journal of the North American Benthological Society* 26:532-545.
- Metzler, G.M., and L.A. Smock, 1990. Storage and dynamics of subsurface detritus in a sand-bottomed stream. *Canadian Journal of Fisheries and Aquatic Sciences* 47:588-594.
- Meyer, J.L., and R.T. Edwards, 1990. Ecosystem metabolism and turnover of organic carbon along a blackwater river continuum. *Ecology* 71:668-677.
- Moss, B., 1977. Adaptations of epipellic and epipsammic freshwater algae. *Oecologia* 28:103-108.
- Mulholland, P.J., C.S. Fellows, J.L. Tank, N.B. Grimm, J.R. Webster, S.K. Hamilton, E. Marti, L. Ashkenas, W.B. Bowden, W.K. Dodds, W.H. McDowell, M.J. Paul, and B.J. Peterson, 2001. Inter-biome comparison of factors controlling stream metabolism. *Freshwater Biology* 46:1503-1517.
- Naiman, R.J., R.E. Bilby, and P.A. Bisson, 2000. Riparian ecology and management in the Pacific coastal rain forest. *BioScience* 50:996-1011.
- O'Conner, N.A., and P.S. Lake, 1994. Long-term and seasonal large-scale disturbances of a small lowland stream. *Australian Journal of Marine and Freshwater Research* 45:243-255.

- Ortiz-Zayas, J.R., W.M. Lewis, Jr., J.F. Saunders, J.H. McCutchan, and F.N. Scantena, 2005. Metabolism of tropical rainforest stream. *Journal of the North American Benthological Society* 24:769-783.
- Peterson, C.G., 1996. Response of benthic algal communities to natural physical disturbance. In: Stevenson, R. J., M.L., Bothwell, and R.L. Lowe (editors). *Algal Ecology: Freshwater Benthic Ecosystems*. San Diego, Academic Press: 375-402.
- Rathbun, R.F., D.W. Stephens, D.J. Schultz, and D.Y. Tai, 1978. Laboratory studies of gas transfer for reaeration. *Journal of Environmental Engineering*. 104:2377-2385.
- Roberts, B.J., P.J. Mulholland, and W.R. Hill, 2007. Multiple scales of temporal variability in ecosystem metabolism rates: results from 2 years of continuous monitoring in a forested headwater stream. *Ecosystems* 10:588-606.
- Rounick, J.S., and M.J. Winterbourn, 1983. Leaf processing in two contrasting beech forest streams: effects of physical and biotic factors on litter breakdown. *Archiv für Hydrobiologia* 96:448-474.
- SAS Institute Inc. 2011. *SAS/STAT® 9.3 User's Guide*. Cary, NC: SAS Institute Inc.
- Stevenson, R.J., 1990. Benthic algal community dynamics in a stream during and after a spate. *Journal of the North American Benthological Society* 9:277-288.
- Stream Solute Workshop, 1990. Concepts and methods for assessing solute dynamics in stream ecosystems. *Journal of the North American Benthological Society* 9:95-119.
- Tank, J.L., E.J. Rosi-Marshall, N.A. Griffiths, S.A. Entekin, and M.L. Stephen, 2010. A review of allochthonous organic matter dynamics and metabolism in streams. *Journal of the North American Benthological Society* 29:118-146.
- Uehlinger, U., 1991. Spatial and temporal variability of the periphyton biomass in a prealpine river (Necker, Switzerland). *Archiv für Hydrobiologia* 123:219-237.
- Uehlinger, U., 2000. Resistance and resilience of ecosystem metabolism in a flood-prone river system. *Freshwater Biology* 45:319-332.
- Uehlinger, U., 2006. Annual cycle and inter-annual variability of gross primary production and ecosystem respiration in a floodprone river during a 15-year period. *Freshwater Biology* 51:938-950.
- Uehlinger, U., and M.W. Naegeli, 1998. Ecosystem metabolism, disturbance, and stability in a prealpine gravel bed river. *Journal of the North American Benthological Society* 17:165-178.

CHAPTER 5. CONCLUSIONS

Synopsis of Previous Chapters

In the previous chapters, I have described several studies using one-station, open-system analyses of diel oxygen curves to determine the rates of ecosystem metabolism in several streams of the coastal plain of southeast Louisiana. Specifically, these studies were conducted at varying temporal and spatial scales to elucidate patterns and potential controls on rates of gross primary production (GPP) and ecosystem respiration (ER). In chapter 2, I investigated four streams seasonally over two years where two of the streams were smaller 2nd order streams with an intact canopy while the other two were slightly larger 3rd order streams with a set-back canopy due to hydrological scouring of the floodplain. The canopy in the 2nd order streams was important in both limiting light to primary producers during periods of leaf on and providing a steady rates of large woody debris (LWD) input and a supply of leaf litter after leaf abscission in fall to the heterotrophic organisms. In chapter 3, I described a 2-year spatial snapshot of the rates of GPP and ER in multiple streams in summer months. Both GPP and ER rates were affected by stream size as the riparian canopy limited light for autotrophs but provided an adequate source of organic matter (OM) for respiration while in larger systems, increased light allowed GPP rates to increase and provided a supplemental source of respiration. In chapter 4, flooding, and one especially extreme event, Hurricane Gustav, affected the rates of GPP and ER by scouring the stream of algae, resorting sediments, and through the input, resuspension, burial, or removal of OM.

Future Directions and Conclusions

Stream systems throughout the world continue to be stressed by pervasive watershed land use changes related to agricultural, municipal, industrial, and infrastructural development (e.g., Nelson et al., 2009; Tank et al., 2010). Moreover, these changes are occurring against the backdrop of significant climate change that will likely have profound impacts on precipitation intensity and frequency (e.g., Dettinger, 2011), as well as water availability and water use (Hansen et al., 2012). Measurements of stream metabolism have the potential to provide important information on the consequences of these disturbances to basic stream processes, which ultimately determine the autochthonous energy and nutrients available to support lotic biodiversity. Recently, Marcarelli et al. (2010) predicted that climate change effects on flow rather than temperature would have the most important impacts on metabolism rates in a 5th order river in Idaho. However, this is the only study that has linked climate change and stream hydrology based on open-system metabolism measurements. Other studies have attempted to assess the potential effects of global warming on stream metabolism, especially in subarctic or alpine streams that are especially susceptible to temperature change (e.g., Acuña et al., 2009; Rasmussen et al., 2011). In this sense, metrics such as stream metabolism may act as a canary-in-the-coal-mine for the losses of ecosystem function due to climate change (cf. Williamson et al., 2008).

Numerous open-system studies of stream GPP and ER in North America, Europe, and Australia (and a few studies in the tropics, e.g., Acuña et al., 2004; Ortiz-Zayas et al., 2005) have been integral in the development of stream metabolism theory. This avenue of research could also provide relatively sensitive indices for regional assessments of stream impacts caused by climate change, hydrological alterations, and watershed land use modifications. However, more

studies are needed in reference (unimpaired) systems to clarify regional metabolism patterns and better distinguish impaired streams (Izagirre et al., 2008). In addition, temporal variability should be an integral part of the design of future studies, as GPP and ER rates can vary from year to year (Young and Huryn, 1996; Acuña et al., 2004; 2007) and season to season (Roberts et al., 2007; Izagirre et al., 2008; Chapter 2 and 4). Stochastic disturbance events, such as storms, can also affect temporal rates of GPP and ER by scouring benthic algae (e.g., Uehlinger, 2006; Chapter 4) and through the input of OM from the watershed or riparian zone (e.g., Roberts et al., 2007) or export of OM downstream (e.g., Acuña et al., 2004; Chapter 4), but can only be monitored through continuous studies. Lastly, the effects of hydrologic modification on the effects of longitudinal patterns of ecosystem metabolism have only been assessed in very few studies (e.g., Uehlinger et al., 2003), but will likely be a profitable study path in the future.

Although considerable research has focused on the combination of effects of light, nutrients, and herbivory on algal biomass in experimental flumes, the effects of these factors on GPP and ER rates have received much less attention (but see Hill et al., 2009). Open-system methods would be particularly effective in studying these factors in smaller systems such as experimental flumes or side channels where light availability, discharge (disturbance) rates, nutrient levels, surface diffusion, and herbivore densities could be controlled. For example, Gerull et al., (2012) manipulated disturbance depth in sand-substrate experimental flumes and found that increased sediment mixing stimulated microbial respiration and resulted in a temporary shift towards heterotrophy in mature sediment communities.

The use of riparian buffers to protect riverine systems from watershed activities has been advocated for some time; however, Houser et al. (2005) determined that the maintenance of riparian buffers was insufficient to protect stream function from watershed disturbance.

Additionally, many studies have shown that agricultural and urban land use, and even the legacy of such land uses, can have an impact on both GPP and ER (e.g., Wiley et al., 1990; Young and Huryn, 1999; Houser et al., 2005; Bott et al., 2006; McTammany et al., 2007; Izagirre et al., 2008; Bernot et al., 2010; Frankforter et al., 2010; Chapter 3). In a review of multiple studies of primary and secondary production and ecosystem respiration, Finlay (2011) separated the streams into those with human-dominated watersheds versus reference systems and determined that the linearity of all three metrics broke down in streams with human-dominated watersheds. As such, the analysis of ecosystem metabolism in systems and/or regions that have both human-dominated and pristine watersheds as well as those with changes to land use patterns represent fruitful areas for future research. Additionally, many studies have pointed out the need to assess ecosystem metabolism in larger systems (Izagirre et al., 2008; Finlay, 2011).

Lastly, open-system measurements of stream metabolism can provide important insights into the effects of non-native organisms on stream biotic structure and function. For example, Hall et al. (2003) quantified GPP and ER with open-system methods in Polecat Creek, Wyoming, and found that 75% of GPP was being consumed by the exotic snail *Potamopyrgus antipodarum*. In the San Marcos River, Texas, abundant sucker-mouth catfish (*Hypostomus plectostomus*) are likely having significant impacts on trophic structure and fish assemblage composition, as the diet of this exotic benthivore is composed primarily of algae and detrital OM (Pound et al., 2011). Studies of stream metabolism in field exclosures would be particularly instructive in determining not only the effects of this exotic species on the San Marcos River fish assemblage, but also predicting the success and effects of additional invasions in other warmwater Texas streams. Although not an exotic organism, the effects of 17-year cicada emergence on two streams in Maryland were also assessed with open-system determinations of

ER (Menninger et al., 2008). Interestingly, the detrital subsidy of decomposing cicadas resulted in a short-term doubling of ER in the study streams during the flight season.

In conclusion, it is clear that open-system metabolism studies have contributed much to the theory of primary production and organic matter processing in lotic systems. Results of these studies indicate that light availability is the most important factor controlling GPP, which can either be enhanced by nutrients or depressed by flooding. Likewise, the supply of OM in streams seems to be one of the most important factors fueling ER, with other factors such as hyporheic zone connectivity or watershed nutrient inputs and organic pollution augmenting these rates. Variations in open-system methodologies have been developed (e.g., one-station v. two-station), and should be used when stream conditions call for one method over another. Hopefully, stream metabolism rates estimated with these methods will enjoy wider application in future studies of the effects of climate change, watershed and riparian modifications, and invasive species on stream function and health.

References

- Acuña, V., A. Giorgi, I. Muñoz, U. Uehlinger, and S. Sabater, 2004. Flow extremes and benthic organic matter shape the metabolism of a headwater Mediterranean stream. *Freshwater Biology* 49:960-971.
- Acuña, V., A. Giorgi, I. Muñoz, F. Sabater, and S. Sabater, 2007. Meteorological and riparian influences on organic matter dynamics in a forested Mediterranean stream. *Journal of the North American Benthological Society* 26:54-69.
- Acuña, V., A. Wolf, U. Uehlinger, and K. Tockner, 2008. Temperature dependence of stream benthic respiration in an Alpine river network under global warming. *Freshwater Biology* 53:2076-2088.
- Bernot, M.J., D.J. Sobota, R.O. Hall, P.J. Mulholland, W.K. Dodds, J.R. Webster, J.L. Tank, L.R. Ashkenas, L.W. Cooper, C.N. Dahm, S. Findlay, S.V. Gregory, N.B. Grimm, S.K. Hamilton, S.L. Johnson, W.H. McDowell, J.L. Meyer, B.J. Peterson, G.C. Poole, H.M. Valett, C. Arango, J.J. Beaulieu, A.J. Burgin, C. Crenshaw, A.M. Helton, L. Johnson, J.

- Merriam, B.R. Niederlehner, J.M. O'Brien, J.D. Potter, R.W. Sheibley, S.M. Thomas, and K. Wilson, 2010. Inter-regional comparison of land-use effects on stream metabolism. *Freshwater Biology* 55:1874-1890.
- Bott, T.L., D.S. Montgomery, J.D. Newbold, D.B. Arscott, C.L. Dow, A.K. Aufdenkampe, J.K. Jackson, and L.A. Kaplan, 2006. Ecosystem metabolism in stream of the Catskill Mountains (Delaware and Hudson River watersheds) and Lower Hudson Valley. *Journal of the North American Benthological Society* 25:1018-1044.
- Dettinger, M., 2011. Climate change, atmospheric rivers, and floods in California – a multimodel analysis of storm frequency and magnitude changes. *Journal of the American Water Resources Association* 47:514-523.
- Finlay, J.C., 2011. Stream size and human influences on ecosystem production in river networks. *Ecosphere*: doi:10.1890/ES1811-00071.00071.
- Frankforter, J.D., H.S. Weyers, J.D. Bales, P.W. Moran, and D.L. Calhoun, 2010. The relative influence of nutrients and habitat on stream metabolism in agricultural streams. *Environmental Monitoring and Assessment* 168:461-479.
- Hall, R.O., J.L. Tank, and M.F. Dybdahl, 2003. Exotic snails dominate nitrogen and carbon cycling in a highly productive stream. *Frontiers in Ecology and the Environment* 1:407-411.
- Hansen, J., M. Sato, and R. Ruedy, 2012. Perception of climate change. *Proceedings of the National Academy of Sciences*. www.pnas.org/cgi/doi/10.1073/pnas.1205276109.
- Hill, W.R., S.E. Fanta, and B.J. Roberts, 2009. Quantifying phosphorus and light effects in stream algae. *Limnology and Oceanography* 54:368-380.
- Houser, J.N., P.J. Mulholland, and K.O. Maloney, 2005. Catchment disturbance and stream metabolism: patterns in ecosystem respiration and gross primary production along a gradient of upland soil and vegetation disturbance. *Journal of the North American Benthological Society* 24:538-552.
- Gerull, L., A. Frossard, M.O. Gessner, and M. Mutz, 2012. Effects of shallow and deep sediment disturbance on whole-stream metabolism in experimental sand-bed flumes. *Hydrobiologia* 683:297-310.
- Izagirre, O., U. Agirre, M. Bermejo, J. Pozo, and A. Elosegui, 2008. Environmental controls of whole-stream metabolism identified from continuous monitoring of Basque streams. *Journal of the North American Benthological Society* 27:252-268.
- Marcarelli, A.M., R.W. Van Kirk, and C.V. Baxter, 2010. Predicting effects of hydrologic alteration and climate change on ecosystem metabolism in a western U.S. river. *Ecological Applications* 20:2081-2088.

- McTammany, M.E., E.F. Benfield, and J.R. Webster, 2007. Recovery of stream ecosystem metabolism from historical agriculture. *Journal of the North American Benthological Society* 26:532-545.
- Nelson, K.C., M.A. Palmer, J.E. Pizzuto, G.E. Moglen, P.A. Angermeier, R.H. Hildebrand, M. Dettinger, and K. Hayhoe, 2009. Forecasting the combined effects of urbanization and climate change on stream ecosystems: from impacts to management options. *Journal of Applied Ecology* 46:154-163.
- Pound, K.L., W.H. Nowlin, D.G. Huffman, and T.H. Bonner, 2011. Trophic ecology of a nonnative population of suckermouth catfish (*Hypostomus plecostomus*) in a central Texas spring-fed stream. *Environmental Biology of Fish* 90:277-285.
- Rasmussen, J.J., A. Baattrup-Pedersen, T. Riis, and N. Friberg, 2011. Stream ecosystem properties and processes along a temperature gradient. *Aquatic Ecology* 45:231-242.
- Roberts, B.J., P.J. Mulholland, and W.R. Hill, 2007. Multiple scales of temporal variability in ecosystem metabolism rates: results from 2 years of continuous monitoring in a forested headwater stream. *Ecosystems* 10:588-606.
- Tank, J.L., E.J. Rosi-Marshall, N.A. Griffiths, S.A. Entekin, and M.L. Stephen, 2010. A review of allochthonous organic matter dynamics and metabolism in streams. *Journal of the North American Benthological Society* 29:118-146.
- Uehlinger, U., 2006. Annual cycle and inter-annual variability of gross primary production and ecosystem respiration in a floodprone river during a 15-year period. *Freshwater Biology* 51:938-950.
- Uehlinger, U., B. Kawecka, and C.T. Robinson, 2003. Effects of experimental floods on periphyton and stream metabolism below a high dam in the Swiss Alps (River Spöl). *Aquatic Sciences* 65:199-209.
- Wiley, M.J., L.L. Osborne, and R.W. Larimore, 1990. Longitudinal structure of an agricultural prairie river system and its relationship to current stream ecosystem theory. *Canadian Journal of Fisheries and Aquatic Sciences* 47:373-384.
- Williamson, C.E., W.K. Dodds, T.K. Kratz, and M.A. Palmer, 2008. Lakes and streams as sentinels of environmental change in terrestrial and atmospheric processes. *Frontiers in Ecology and the Environment* 6:247-254.
- Young, R.G., and A.D. Huryn, 1996. Interannual variation in discharge controls ecosystem metabolism along a grassland river continuum. *Canadian Journal of Fisheries and Aquatic Sciences* 53:2199-2211.
- Young, R.G., and A.D. Huryn, 1999. Effects of land use on stream metabolism and organic matter turnover. *Ecological Applications* 9:1359-1376.

**APPENDIX. SOURCE TABLES FOR VARIOUS ANOVAS USED
IN THIS DISSERTATION**

Table A2.1 ANOVA table for GPP for shaded vs unshaded streams

Source	DF	Mean Square	F-value	p-value
shade	1	45.29	138.02	< 0.01
year	1	4.67	14.25	< 0.01
season	3	5.23	15.96	< 0.01
shade*year	1	5.92	18.04	< 0.01
shade*season	3	9.29	28.30	< 0.01
year*season	3	3.21	9.77	< 0.01
shade*year*season	3	2.10	6.39	< 0.01

Table A2.2 ANOVA table for ER for shaded vs unshaded streams

Source	DF	Mean Square	F-value	p-value
shade	1	112.64	112.64	< 0.01
year	1	14.27	14.27	< 0.01
season	3	41.64	41.64	< 0.01
shade*year	1	6.81	6.81	< 0.01
shade*season	3	12.96	12.96	< 0.01
year*season	3	4.58	4.58	< 0.01
shade*year*season	3	4.57	4.57	< 0.01

Table A2.3 ANCOVA table for ER for shaded vs unshaded streams

Source	DF	Mean Square	F-value	p-value
Shade	1	52.04	80.81	< 0.01
GLA	1	12.33	19.15	< 0.01
Shade*GLA	1	20.07	31.16	< 0.01

Table A2.4 ANOVA table for percent LWD

Source	DF	Mean Square	F-value	p-value
site	3	1.03005	236.87	< 0.01
error	26	0.00435		

Table A2.5 ANOVA table for percent BOM

Source	DF	Mean Square	F-value	p-value
year	1	1.37329821	2.4	0.12
season	3	2.85772001	4.99	< 0.01
site	3	18.99019772	33.17	< 0.01
year*season	3	0.07900412	0.14	0.94
year*site	3	0.78105492	1.36	0.26
season*site	9	0.39094302	0.68	0.72
year*season*site	7	0.32563524	0.57	0.78

VITA

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