

From Carbon to Fish: Understanding Mechanisms of Human Impacts on Freshwater
Ecosystems

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Authorization to Submit Dissertation

This dissertation of Aline Ortega Pieck, submitted for the degree of Doctorate of Philosophy with a major in Water Resources Science and Management and titled “From Carbon to Fish: Understanding Mechanisms of Human Impacts on Freshwater Ecosystems,” has been reviewed in final form. Permission, as indicated by the signatures and dates below, is now granted to submit final copies to the College of Graduate Studies for approval.

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Abstract

Freshwater ecosystems provide essential ecosystem services (e.g. clean water, food production) to society. These services are impacted by human activities, such as agriculture. A critical change resulting from agricultural land use is the alteration of stream ecosystem function through its effects on organic carbon processing (stream metabolism). Carbon is the building block of all organisms and represents the energy fueling ecosystems. Streams also play a key role in the global carbon cycle. Thus, understanding how agriculture modifies metabolism is relevant at both local (e.g. stream ecosystem assessments) and global scales (e.g. carbon exports from streams).

Most of our knowledge on stream metabolism derives from temperate latitudes. Metabolic drivers in tropical regions have unique regimes that could lead to particular responses to agriculture, yet we have limited empirical evidence of the magnitude of metabolism in these regions. At larger scales, it is unknown whether metabolic responses to agriculture differ between world biomes or agricultural types. Thus, Chapter 1 presents an empirical study of stream metabolism in a humid-tropical watershed. I specifically ask, what is the magnitude of metabolism in streams draining abrupt forest-agricultural boundaries? Which factors drive metabolic changes? Results show that metabolism increases with higher light in agricultural areas but metabolic rates are generally low in areas adjacent to forests. Chapter 2 is a global meta-analysis where I ask, does stream metabolism in biomes with contrasting types of riparian vegetation respond differently to agriculture? Does metabolism differ between croplands and pastures? Results show that biome light regimes determine metabolic vulnerability and that metabolism differs between food production systems. Chapter 3 is an interdisciplinary modelling effort of fish yields in small reservoirs in semi-arid Africa. Fisheries are essential for population nutrition and resilience but there is a lack tools to estimate yields at large spatial scales. I present a method paring remotely-sensed surface water dynamics with an empirical equation of fish yield that can be used to understand reservoir fisheries across semi-arid landscapes.

This dissertation furthers our understanding of human influences of on freshwater ecosystems. This knowledge may be used to better manage trade-offs between agriculture production and freshwater ecosystem function.

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Dedication

I would like to dedicate this dissertation to my mother Irene Pieck de la Torre. There are no words to describe the power of your love and how fortunate I am for being your daughter. Thank you for always pointing out the flowers, butterflies and mountains. Thank you for always being present.

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Chapter 1: Agricultural influences on the magnitude of stream metabolism in humid tropical headwater streams

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Abstract

The production and respiration of organic carbon in streams (stream metabolism) is a fundamental ecosystem process. The extent to which the magnitude of stream metabolism changes with forest conversion to agriculture in humid tropical headwaters is poorly understood. We measured whole-stream metabolism in headwaters draining forest-agricultural boundaries to investigate metabolic rates in areas with abrupt land use transitions and the role of remnant riparian vegetation. We used linear mixed models to test the hypotheses that gross primary production (GPP) and ecosystem respiration (ER) would be higher in agricultural areas due to higher light availability and nutrient concentrations, respectively. We found a 257% increase in GPP and 30% increase in ER in agricultural stream reaches. GPP was driven by light and ER was mainly controlled by GPP. These results highlight the overriding influence of light in agricultural streams with large fractions of upstream forest cover. Our findings suggest that high riparian canopy cover (~ 90%) is necessary to support stream metabolic rates similar to forests in agricultural areas. This study adds to our understanding of the within-biome variation of metabolism resulting from agriculture, and the potential similarities between forested biomes and the role of tropical streams in the global carbon cycle.

Introduction

Headwaters play an important role in the global carbon (C) cycle because they comprise most of the length of drainage networks and process large amounts of terrestrial C (Cole et al., 2007; Battin et al., 2009). The close association between headwater ecosystems and the surrounding terrestrial environment makes in-stream C processing highly sensitive to agricultural impacts, such as riparian vegetation removal (Meyer & Wallace, 2001; Bernot et al., 2010). Forest conversion to agriculture modifies the rate at which C is produced and consumed within stream ecosystems (Griffiths et al., 2013), and the relative importance of organic C sources (terrestrial vs. in-stream produced) that support these lotic ecosystems

(Dodds, 2006; Hagen et al., 2010). Changes in C sources and processing rates can negatively impact ecosystem services and modify stream ecosystems locally and downstream (England & Rosemond, 2004; Fremier et al., 2013; Hill et al., 2014). For example, increases in stream autotrophic C can lead to poor water quality (Dodds, 2006) and may strongly affect food web structure and ecosystem processes, such as animal production and organic matter flow (Marcarelli et al., 2011). At global scales, changes in stream C cycling may modify CO₂ evasion to the atmosphere (Hotchkiss et al., 2015).

Whole-stream metabolism refers to the rates at which ecosystems produce and consume organic C via gross primary production (GPP) and ecosystem respiration (ER). For this reason, stream metabolism is used as a functional metric to understand in-stream C processing drivers and integrative influences of agricultural land use (Williamson et al., 2008; Young et al., 2008). Light availability is an overriding driver of GPP (Mulholland et al., 2001; McTammany et al., 2007) and is largely controlled by riparian vegetation (Bunn et al., 1999; Bernot et al., 2010; Burrell et al., 2013). Other factors, such as larger nutrient inputs may lead to increases in GPP, while high stream flows can temporarily limit GPP (Mulholland et al., 2001; Acuña et al., 2004). Temperature, nutrients and organic matter, among others, drive ER (McTammany et al., 2007; Elosegi & Sabater 2012; Yates et al., 2013). The main factors controlling stream metabolism are well documented and in general appear to coincide across latitudes and biomes (Boulton et al., 2008; Tank et al., 2010). However, much of our understanding of agricultural impacts on stream metabolism derives from temperate regions (Staeher et al., 2012), with only a few studies in tropical ecosystems (Bunn et al., 1999; Mulholland et al., 2001; Bernot et al., 2010; Gücker et al., 2009; Bott & Newbold, 2013; Masese et al., 2016). Thus, the extent to which agriculture modifies the magnitude of stream metabolism in humid tropical streams remains understudied (Griffiths et al., 2013).

Although the drivers of stream metabolism are likely the same in tropical and temperate systems, it is unclear how the magnitude of metabolic rates might change in the humid tropics in response to land use change. Key drivers shaping stream metabolism in humid tropical regions such as light, temperature and stream flow have unique regimes (i.e., timing and magnitude) that may distinctly influence metabolism when forest cover is lost. In particular, the humid tropics naturally undergo small seasonal temperature variation and solar irradiance and precipitation levels are consistently high (Lewis, 2008). These environmental conditions

lead to high terrestrial productivity, dense forest canopies that block the majority of incoming radiation, and a consistent subsidy of terrestrial organic matter to streams (Davies et al., 2008). The constant inputs of terrestrial organic matter, coupled with warm water temperatures and low irradiance levels, maintain a strong terrestrial–aquatic ecosystem link and support high metabolic activity and stream net heterotrophy year–round (Ortiz-Zayas et al., 2005). For this reason, headwater riparian vegetation in agricultural watersheds likely has a major influence over stream metabolism (Wantzen et al., 2008) and, as in terrestrial systems, the spatial patterns of forest cover removal are likely important in determining the effects of agriculture on stream C dynamics (Chaplin-Kramer et al., 2015).

In intensively managed tropical areas, the boundaries between forests and agricultural lands are frequently abrupt and riparian vegetation is either entirely removed or significantly reduced for agriculture (Ramírez et al., 2008). As a result, terrestrial organic matter inputs decrease and stream communities become exposed to high solar irradiance and warmer water temperatures (Bunn et al., 1999). In addition, streams commonly receive excessive nutrient and sediment inputs (Pringle et al., 2000; Carlson et al., 2014). All together, these changes can greatly alter stream metabolism; yet, we lack empirical evidence of the metabolic changes that occur in abrupt forest–agricultural boundaries and the role of remnant riparian vegetation.

In this study, we measured headwater stream metabolism in a humid tropical region in central Costa Rica during the low flow season. Our main objectives were to: 1) quantify metabolism in forested and agricultural stream reaches and 2) determine whether remnant riparian vegetation canopy cover in agricultural areas influences the degree of stream metabolism change. We hypothesized that the magnitude of GPP and ER would be greater in agricultural than forested stream reaches mainly due to higher light availability and nutrient concentrations, respectively. We discuss our findings in the context of changes in the magnitude of stream metabolism by comparing them to studies from other humid tropical and temperate forested streams. Lastly, we discuss the implications for management of tropical headwaters in agricultural areas.

Methods

Study area

The study area is located 650–760 m above mean sea level in the Jiménez Cantón, central Costa Rica (Fig. 1.1). The region is in the premontane rain forest life zone (Holdridge, 1967) and belongs to the Volcánica Central Talamanca Biological Corridor. The underlying geology consists of quaternary deposits (Montero et al., 2013) with a mix of small to large alluvium, colluvium and bedrock. Rainfall is intense and consistent between May and December with a short less wet period from January to April (seasonal monthly mean of 270 and 140 mm, respectively). The mean annual temperature is 22°C and exhibits limited seasonal variation (CATIE meteorological station, unpublished data). Land cover is primary forests (dominated by *Vochysia allenii* Standl. & L. O. Williams, *Pourouma bicolor* Mart., and *Hedyosmum scaberrimum* Standl.), intensively managed sugarcane fields and a few patches of secondary forests regenerating post abandonment of coffee farms. Primary forests are mainly present on steep hills. Agriculture dominates the valleys although it is also present in high gradient terrain. The selected area provided an ideal setting for our research given that the change from forest to agriculture cover in this watershed is abrupt and the only remnant woody vegetation in agricultural areas is found along stream banks and mainly consists of sparse (i.e. 15–30 m spacing) remnant poró trees (*Erythrina poeppigiana* (Walp.) O.F. Cook) with heights of approximately 15–20 m. All streams ran through forested areas in the uplands and through agriculture downstream (Fig. 1.1).

Study design

To assess the magnitude of GPP and ER, and explore the influence of remnant riparian vegetation, we chose six 1st–2nd order headwater streams. In these six streams, we selected a set of study reaches ($n = 9$) consisting of three forested and six agricultural with varying amounts of remnant riparian vegetation (Fig. 1.1). The downstream end of forested, and the upstream end of agricultural reaches were located 25–100 m away from the intersection between these two land uses. The reason for our unbalanced study design was the limited availability of forested sites with adequate characteristics for measuring stream metabolism. Specifically, we selected the longest possible reaches based on access and suitability, mainly avoiding tributary and groundwater inflows, and areas where channel characteristics would

likely cause high reaeration rates, such as drops or waterfalls. We placed a staff gauge in all stream reaches and recorded water levels daily to ensure discharge did not change during sampling periods based on the assumption that constant water depth indicated constant discharge. We conducted the study at base flows and collected data between February and April of 2014. We measured stream metabolism for two to five days at each study reach. The 2014 season was particularly dry compared to previous dry seasons in the region (CATIE meteorological station, unpublished data).

Field measurements and laboratory analyses

Study reach geomorphology, hydrology and water chemistry We conducted a Wolman pebble count for 100 randomly chosen particles over the entire selected stream reach (Wolman, 1954). We measured the *b* axis with a gravelometer or a measuring tape for boulders and calculated the median grain size (D_{50}). We obtained a gross estimate of percent streambed slope using a clinometer. We measured wetted width at 14 locations along the reach; at each location, we also measured water depth across the channel every 10 cm.

We measured water velocity and discharge (Q) with the time–concentration curve method (Kilpatrick et al., 1989). We injected a salt slug (i.e. NaCl) and recorded water specific conductance (SC) at the upstream and downstream stations (Professional Plus Multiparameter Meter, YSI, Yellow Springs, Ohio). Prior to the slug injections, we calibrated the SC probes to standards and to each other. All discharge measurements occurred within 1 week prior to measuring metabolism.

To quantify nutrient concentrations, we sampled water within 2 weeks of stream metabolism assessments at the downstream end of each study reach. We stored samples in a cooler and transported them to the laboratory for immediate water chemistry analyses. Prior to analyzing we filtered all water samples (Whatman, 0.7 μm GF/F). We measured soluble reactive phosphorus (SRP) with the stannous chloride colorimetric method (APHA, 1995) using a UV–V spectrophotometer (Thermo Spectronic Helios Alpha, United Kingdom). We determined ammonium ($\text{NH}_4^+\text{-N}$) and nitrate ($\text{NO}_3^-\text{-N}$) concentrations with a distillation–titration method, using boric acid as the receiving solution; in addition, for nitrates we used Devarda’s alloy (APHA, 1975). We obtained a value of dissolved inorganic

nitrogen (DIN) by summing NO_3^- -N and NH_4^+ -N concentrations. Detection limits were $0.3 \mu\text{g SRP-P L}^{-1}$ for SRP, 0.1 mg N L^{-1} for NO_3^- -N, and 0.05 mg N L^{-1} for NH_4^+ -N.

Light environment and land use We measured daily photosynthetically active radiation (PAR) concurrently with stream metabolism by placing PAR sensors adjacent to the channel 10 cm above water level and recording 1-min average values every 15 min (HOBO Micro Station Data Logger, ONSET, Bourne, Massachusetts). In addition, we estimated the percentage of canopy cover at 10 random locations along the channel with a spherical densitometer 0.5 m above the water surface, and averaged all points to get a mean value. Given the lack of accurate land use maps for our study region, we delineated the sub-basin boundaries of each study reach using ArcHydro in ArcGIS 10.2 (ESRI, Redlands, California). We then used a BirdsEye image from 2005 to manually classify land use and estimate the proportion of agricultural land cover within each drainage (AGLC). We confirmed that no significant changes in land cover and riparian vegetation had occur since 2005 using Google Earth and by interviewing the sugar cane cooperative directives.

Periphyton and benthic organic matter We sampled periphyton from 20 randomly selected rocks per study reach no more than 1 week before or after measuring stream metabolism. We used a standard protocol for estimating the standing stock of periphyton from each rock (Steinman et al., 2006). We scraped each rock with a wire brush using a known amount of water to create a slurry and divided the slurry into 2 subsamples of equal volume. We filtered each subsample onto a pre-weighed and pre-combusted glass fiber filters; we stored one for Chlorophyll *a* (Chl-*a*) and the other for ash free dry mass (AFDM) analyses. We wrapped the filters in aluminum foil and kept them at 4°C for a maximum of 3 weeks prior to processing. For the Chl-*a* extraction we used the method proposed by Ritchie (2006) which does not include correction for pheophytin. We extracted Chl-*a* by adding 90% ethanol and refrigerating for 24 h. We then centrifuged the samples at 3000 rpm for 15 min and read Chl-*a* absorbance in a spectrophotometer (Spectronic Helios Alpha Beta UV-Visible Spectrophotometer, Thermo Scientific). For the AFDM analyses, we oven-dried the filters for 24 h at 105°C and weighed them. We then incinerated the filters at 500°C for 1 h, and re-weighed them. At each study reach, we estimated the proportion of coarse particulate

organic matter (CPOM) covering the streambed by placing a 0.5 by 0.5 m quadrat and visually estimating cover at 10 random locations and averaging all values.

Reaeration coefficient We measured reaeration coefficients (KO_2) in six of the nine study reaches within 1 week prior to assessing stream metabolism (Table 1.1). We could not measure KO_2 in the remaining sites due to equipment malfunction. We used the upstream–downstream propane evasion method (Marzolf et al., 1994; Young & Huryn 1998). We determined the injection time needed to reach propane equilibrium plateau concentrations from the salt slug–response curves. Using a commercial propane tank, we injected propane into the water column through a pierced hose. Just above the tank, we injected a solution with salt at a constant rate using a Mariotte bottle for the conservative tracer analyses. The upstream sampling station was located 10 m or more below the injection point to allow the propane and conservative tracer to mix vertically and laterally; we used a slug of fluorescein to visually confirm mixing distances were adequate prior to measuring KO_2 . At both stations, we sampled background concentrations before the injection and collected four samples during plateau in 50 ml glass serum vials. We sealed the samples with 3–pronged rubber stoppers and aluminum crimp–seals and refrigerated them until the gas chromatography analyses. We measured propane concentrations after Bott (2006) using a gas chromatograph with a flame ionization detector (Trace–Ultra Gas Chromatograph, Thermo Scientific, Waltham, Massachusetts). We used the values of SC measured in the field for the conservative tracer estimates (Stream Solute Workshop, 1990). We calculated mean water travel time (t) as the time interval between up and downstream stations reaching half plateau concentrations and screened for groundwater inputs by determining whether dilutions of the plateau concentration at the downstream stations occurred. To estimate KO_2 in the three reaches with no field KO_2 data, we explored different relationships between KO_2 as a function of Q and slope using the six study reaches where these three variables were measured (Table 1.1). The best fit resulted from a polynomial relationship between KO_2 and Q ($R^2 = 0.76$) with the equation:

$$KO_2 = -0.7681 Q^2 + 32.182 Q + 18.438$$

At these three sites, we calculated t from the slug–response curves as the elapsed time between the centroids of the area under the curve of the slug mass at the upstream and

downstream stations (Kilpatrick et al., 1989). In addition, we estimated groundwater inputs by comparing upstream and downstream Q values.

Stream metabolism We calculated stream metabolism with the open water technique measuring diel changes of dissolved oxygen concentrations (Odum, 1956). We used the 2–station method and computed metabolic rates following the protocol of Bott (2006). We placed dissolved oxygen (DO) and water temperature probes (U26 HOBO Dissolved Oxygen Logger, ONSET, Bourne, Massachusetts) in the thalweg at the upstream and downstream station of the study reaches, and logged values every 10 min. Before deployment, we calibrated the sensors following manufacturer’s requirements at 100% saturated air; we then placed both probes at the same location to account for differences in DO measurements. We measured barometric pressure concurrently with DO (HOBO Micro Station Data Logger, ONSET, Bourne, Massachusetts). We calculated the mean hourly nighttime ER rates and extrapolated the values to the daylight hours to get daytime ER estimate. We corrected the rate of change in DO concentrations for water temperature and KO_2 (Elmore & West, 1961). We obtained GPP by adding the average nighttime ER value to the net oxygen change during the day and converted these rates to areal units by multiplying them by the mean stream depth (Bott, 2006). We computed net ecosystem production (NEP) by subtracting ER from GPP. We calculated the ratio of GPP to ER (P/R) to inspect the relative importance of autochthonous and allochthonous C sources (Meyer, 1989).

Statistical Analyses

We used the Spearman’s rank correlation to explore bivariate correlations among measured environmental variables (Table 1.1), as well as between these variables and metabolic parameters. Variables with several observations per study reach were averaged prior to testing for correlation with variables with only one observation such as canopy cover.

Given our unbalanced study design (three forested and six agricultural study reaches) and the lack of spatial independence between study reaches (Fig. 1.1), we used linear mixed models to inspect the drivers of GPP and ER (Pinheiro & Bates, 2000; Zuur et al., 2009). This approach allowed us to account for spatial autocorrelation by including *stream* as a random effect. We also included *study reach* as a random factor in order to include all daily metabolism measurements performed at each study reach, rather than single averaged value, and to avoid

pseudoreplication issues. The sum of all daily stream metabolism estimates across study reaches was 31, where the number of days measured per study reach ranged from two to five. Given the relatively small sample size for constructing linear mixed models ($n = 31$), we first standardized the set of independent variables potentially driving stream metabolism (PAR, CPOM, DIN, SRP, water temperature and canopy cover), and performed a principal component analysis (PCA). The goal of the PCA was to reduce the set's dimensionality by collapsing the variables into individual PC to avoid multicollinearity issues, and to use the PC scores as predictor variables (i.e. fixed effects) in the GPP and ER linear mixed models. We did not include the proportion of agricultural land cover within the study reaches' drainage area (AGLC) in the PCA because we were interested in representing the proximal drivers of stream metabolism and this variable provides an integrated measure of land use influences on stream metabolism (Allan, 2004). Instead, we included AGLC as a separate predictor variable. We used the Kaiser's criterion (i.e., factors with scores >1) to establish the number of PC to extract and include in the linear mixed models. We used the variable's loadings on each axis to determine the characteristics represented by each PC. Based on the Kaiser's criterion, we retained the scores of PC1 and PC2 to use as fixed effects. Together PC1 and PC2 explained 69% of the variance of the set of explanatory variables included in the PCA (Table 1.2). PC1 was mainly associated with variables associated with the light environment, while PC2 was associated with water temperature and nutrients (Table 1.2).

Based on the interpretation of the PCA results, the full model of GPP included PC1, PC2 and AGLC as fixed effects. The full model of ER included GPP, PC2 and AGLC. We did not include PC1 in the ER model given that light is an indirect control of ER mainly through its effect on GPP and water temperature. Explanatory variables of both GPP and ER models showed no collinearity (variance inflation factors < 2) (Zuur et al., 2009). Models were fitted using the restricted maximum likelihood (REML) approach (Zuur et al., 2009) using the *nlme* R package (Pinheiro et al., 2016; R development Core Team, 2016). We inspected deviations from the analysis assumptions using model diagnostic plots (Pinheiro & Bates, 2000). We included a variance function in both GPP and ER models to account for heterogeneity of variance (Pinheiro & Bates, 2000; Zuur et al., 2009). We determined the most parsimonious fixed effect structure comparing nested models, using the maximum likelihood test and the Akaike's Information Criterion corrected for small sample sizes (AICc). We re-fitted the best

GPP and ER models with REML and re-inspected model diagnostic plots (Zuur et al., 2009). All statistical analyses were performed in R software (version 3.3.1; R Development Core Team, Vienna, Austria).

Results

Physical and chemical characteristics of study reaches

No changes in discharge were recorded during metabolism measurements. Time of travel ranged from 12 to 56 minutes across sites and groundwater inflows were either not detected or negligible (Grace & Imberger, 2006). All study reaches were shallow and average channel width ranged from 94 to 193 cm (Table 1.2). Canopy cover was correlated with PAR ($r = -0.92$, $P < 0.001$). In particular, canopy cover in forested reaches was $> 89\%$, where the maximum daily PAR recorded was $1.6 \text{ mol m}^{-2} \text{ d}^{-1}$ (Table 1.2). Canopy cover and PAR in agricultural reaches with remnant riparian vegetation ranged from 52 to 76% and 1.9 to $12.7 \text{ mol m}^{-2} \text{ d}^{-1}$, respectively. The highest PAR was observed at sites with no woody riparian vegetation with values up to $41 \text{ mol m}^{-2} \text{ d}^{-1}$. Given the proximity of all agricultural reaches to the forest edge, AGLC did not exceed 12%. The only significant correlation between AGLC and other physical or chemical variables occurred between canopy cover ($r = -0.88$, $P = 0.001$) and PAR ($r = 0.76$, $P = 0.01$). In general, NO_3^- -N concentrations were moderate (0.1 – 0.21 mg L^{-1}) and NH_4^+ -N was only detected in two agricultural reaches at 0.1 mg L^{-1} . SRP concentrations were high at all sites ranging from 0.1 to 0.25 mg L^{-1} . Water temperature was similar across reaches, averaging $21.0 \pm 0.8^\circ\text{C}$.

Organic matter standing stocks

Average Chl-*a* and AFDM across sites were significantly correlated ($r = 0.75$, $P = 0.01$), and the lowest and highest values of these two variables corresponded to forested and agricultural study reaches, respectively. Chl-*a* was also correlated with AGLC ($r = 0.75$, $P = 0.01$). AFDM was correlated with PAR ($r = 0.93$, $P < 0.001$), AGLC ($r = 0.86$, $P = 0.002$), and canopy cover ($r = -0.7$, $P = 0.04$). CPOM did not vary in a discernable pattern across sites and was not significantly correlated with any physical or chemical variable. The highest CPOM (40% cover) was observed in study reach 3Ag given that sugarcane residues had

partially covered the streambed, likely reducing the amount of PAR reaching the streambed (Table 1.1).

Stream metabolism

In general, metabolic rates were low (Fig. 1.2). Specifically, GPP ranged from 0.03 to 1.01 g O₂ m⁻² d⁻¹ and ER from 0.22 to 1.24 g O₂ m⁻² d⁻¹ (Fig. 1.3a, b). GPP and ER were significantly correlated ($r = 0.47$, $P = 0.008$). Significant correlations between metabolic parameters and environmental variables are shown in Table 1.3; among these, the strongest positive correlations were found between GPP and Chl-*a* ($r = 0.76$, $P = 0.02$), GPP and AFDM ($r = 0.68$, $P = 0.04$), and GPP and NO₃⁻-N ($r = 0.69$, $P = 0.04$). GPP was negatively correlated with CPOM ($r = -0.68$, $P = 0.04$). ER was only associated with water temperature ($r = 0.43$, $P = 0.02$). NEP was negative in all but two agricultural study reaches (Fig. 1.3c), and was correlated with PAR ($r = 0.52$, $P = 0.002$). Overall, GPP and ER were lower in forested than in agricultural study reaches (Fig. 1.4a, c). Mean GPP in forested vs. agricultural reaches was 0.16 ± 0.2 and 0.57 ± 0.27 g O₂ m⁻² d⁻¹. Mean ER was 0.61 ± 0.34 g O₂ m⁻² d⁻¹ in forested sites and 0.79 ± 0.26 g O₂ m⁻² d⁻¹ in agricultural sites. These changes represent a 257% increase in GPP and 30% increase in ER. Average P/R in forested and agricultural study reaches was 0.26 and 0.76, respectively (Fig. 1.4d).

The best statistical model of GPP only included PC1 as a fixed factor, meaning that variation in GPP was mainly determined by PAR and canopy cover (Table 1.2 and 4; Fig. 1.5a). The best model of ER included GPP and PC2 (i.e. water temperature + DIN) as fixed factors and GPP had higher coefficients than PC2 (Table 1.4; Fig. 1.5b, c).

Discussion

This study contributes to our understanding of how the conversion of tropical forests to intensive agriculture modifies the magnitude of stream metabolism. Our findings show that headwaters draining forest-agricultural boundaries undergo increases in metabolic rates mainly due to higher light availability resulting from riparian deforestation. The 2.5-fold increase in GPP found in our study area, likely has implications for other ecosystem process and overall stream ecosystem function. The proportion of forest cover within the drainage

area of agricultural reaches is likely a key factor determining the relative influence of stream metabolism drivers and the absolute magnitude of metabolic rates.

Our data show that increases in the magnitude of stream metabolism occur when streams begin to drain agricultural areas with reduced or absent riparian vegetation. The higher GPP observed with increases in light availability as small as $1 \text{ mol m}^{-2} \text{ d}^{-1}$ and canopy cover $< 76\%$ suggests that stream autotrophic communities were strongly light limited (Table 1.1; Fig. 1.3a). This result is similar to a threshold suggested by Bunn et al. (1999), where less than 73% canopy cover lead to significantly higher GPP. The fact that increases in GPP were observed at low daily PAR values of $0.9 \text{ mol m}^{-2} \text{ d}^{-1}$ supports previous research suggesting that streams in the humid tropics may have high photosynthetic efficiencies (Bernot et al., 2010). The overriding influence of light over GPP found in this study (Table 1.4; Fig. 1.5a) is in agreement with a large body of research (e.g. Mulholland et al., 2001; Bernot et al., 2010; Burrell et al., 2013). Hence, our results stress the importance of dense canopies in tropical headwaters influenced by agricultural land use, especially in areas where the magnitude of GPP is strongly controlled by riparian shading (McTammany et al., 2007; Burrell et al., 2013). Overall, these findings support our hypothesis that light is a first-order control on GPP in our study area.

Our results also show that light exerted an indirect control over ER through its effect on GPP (Fig. 1.5b). This relationship has been previously shown in streams with no light limitation (e.g. Bunn et al., 1999; Yates et al., 2013) and suggests that ER was dominated by autotrophic respiration (Bernot et al., 2010). Alternatively, ER could have been influenced by GPP due to leaching of organic compounds derived from photosynthesis, which may stimulate heterotrophic respiration (Hall & Beaulieu, 2013; Huryn et al., 2014). The significance of PC2 in the statistical model of ER indicates that ER also varied due to increases in heterotrophic metabolism likely promoted by warmer water temperature and perhaps DIN concentrations (Table 1.2) (Sinsabaugh, 1997; Gücker et al., 2009). The limitation of the PCA approach is that it is difficult to separate the effect of these two variables (Table 1.2). Given that the effect of PC2 in the model of ER was smaller compared to that of GPP, we rejected our hypothesis that nutrients mainly drive ER in our study area. We note that our findings only illustrate a fraction of the annual patterns of stream metabolism. During the wetter season, other factors such as high flows, could exert a stronger influence than light (Acuña et al., 2004) and lead to

changes in the relative importance of stream metabolism drivers (Masese et al., 2016). Reduced riparian vegetation cover in our study area shifted the relative importance of C sources towards greater autotrophy (Fig. 1.4d). We found evidence suggesting that the contribution of autochthonous C to the energy base was larger in agricultural than in forested reaches given that all but one agricultural reaches had a P/R > 0.5, while the three forested reaches had a P/R < 0.5 (Meyer, 1989). Given the variability of stream metabolism over different temporal scales (Roberts et al., 2007), assuming an annual constant P/R would likely overestimate the levels of autotrophy (Izagirre et al., 2008; Griffiths et al., 2013). However, the implications of our results are highly relevant given that headwaters represent the starting point of the drainage network. The effects of local changes in the sources of C and processing rates during the dry season potentially cascade up through food webs and modify stream communities and ecosystem function, both locally and downstream (Wipfli et al., 2007; Lorion & Kennedy, 2009). The negative NEP found at the majority of our sites indicates that despite the increase in autotrophy in agricultural reaches, most stream ecosystems remained net consumers of energy and sources of atmospheric CO₂ (Hotchkiss et al., 2015).

Compared to similarly sized humid tropical streams draining forests or row-crop agriculture, absolute metabolic rates in our study area were similar or below previously reported values (Fig. 1.2) (Mulholland et al., 2001; Ortiz-Zayas et al., 2005; Bernot et al., 2010; Bott & Newbold, 2013; Masese et al., 2016). Particularly, average GPP in forested reaches (0.16 g O₂ m⁻² d⁻¹) was within the range previously found in other streams of < 0.1 – 1.7 g O₂ m⁻² d⁻¹ (Fig. 1.4a) (Mulholland et al., 2001; Masese et al., 2016). Mean GPP in agricultural reaches (0.57 g O₂ m⁻² d⁻¹) (Fig. 1.4a) was lower than the 3.6 – 11.7 g O₂ m⁻² d⁻¹ range previously reported for other agricultural streams (Bernot et al., 2010; Masese et al., 2016). Average ER at our forested sites (0.61 g O₂ m⁻² d⁻¹) was also low but within the range of 0.4 – 13.7 g O₂ m⁻² d⁻¹ previously found by other studies in humid tropical headwaters (Fig. 1.4c). Mean ER in agricultural sites (0.79 g O₂ m⁻² d⁻¹) (Fig. 1.4b) was much lower than in a similar Puerto Rican stream where ER was 5.3 g O₂ m⁻² d⁻¹ (Bernot et al., 2010), and five Kenyan headwaters where ER ranged from 4.8 to 20.2 g O₂ m⁻² d⁻¹ (Masese et al., 2016).

We suggest that the main factor leading to the low stream metabolism in agricultural reaches compared to previous studies was the fraction of agricultural land cover (AGLC).

Specifically, agriculture's influence over stream metabolism has been shown to increase with

an increasing proportion of cover within a watershed (Yates et al., 2013; Burrell et al., 2013). Therefore, the small AGLC in our agricultural reaches (0.1–12%) due to their proximity to the forest edge, may have led other drivers of stream metabolism to have a minor influence. AGLC in the studies by Bernot et al. (2010) and Masese et al. (2016) was > 30%, and in several cases exceeded 70%. Accordingly, NO_3^- -N concentrations in their studied agricultural streams were at least twice as high than in this study (Bernot et al., 2010), and reached up to 6.1 mg L^{-1} (Masese et al., 2016). We acknowledge we cannot infer nutrient limitation without nutrient uptake data (Dodds, 2003); yet the high concentrations of SRP, presumably resulting from the volcanic bedrock leaching (Lewis, 2008), compared to NO_3^- -N concentrations, could indicate that our study reaches were N-limited (Keck & Lepori, 2012). ER in forested and agricultural reaches might have also been lower than in other studies due to differences in CPOM stocks; however, given that we only made visual estimations of CPOM streambed cover, we are unable to compare our results to studies with measures of mass per area. Overall, these findings provide empirical evidence of the magnitude of tropical stream metabolism in forest–agricultural boundary areas and inform the degree to which the magnitude of stream metabolism may increase when environmental changes resulting from agriculture are dominated by increases in light.

Metabolic rates in this study fell within the range of headwater stream metabolism in temperate forests and forest areas converted to row–crop agriculture (e.g., Lamberti & Steinman 1997; Mulholland et al., 2001; Bott et al., 2006; Bernot et al., 2010). This finding supports the idea that ecosystem processes may not fundamentally differ between forests in tropical and temperate latitudes (Boulton et al., 2008). However, the base flow season on which we base the comparison of our results, likely represent the periods of greatest resemblance in stream metabolism drivers across latitudes. Specifically, base flows are generally associated with flow stability, high irradiance levels and warm water temperatures (Sinsabaugh, 1997; Mulholland et al., 2001; Acuña et al., 2004). We argue that if the magnitude of stream metabolism differs between latitudes, then this pattern may only be observed with measurements spanning longer periods because tropical regions exhibit smaller seasonal variation temperate regions. Thus, the relevance of an increase in the magnitude of tropical stream metabolism may rely more in factors such as the constant warm water temperatures that could lead to yearly–sustained and potentially higher annual metabolic rates

(DeNicola, 1996; Sinsabaugh, 1997). Further research addressing the variability of stream metabolism across seasons is needed to fully explore these differences.

Riparian forests in agricultural lands provide multiple ecosystem services over a relatively small area (Broadmeadow & Nisbet, 2004; Fremier et al., 2013). Yet protection and restoration of riparian vegetation is uncommon in most countries in the world due to economic constraints and the lack of enforcement (Hickey & Doran, 2004). Here, we add a potential motivation to protecting or planting headwater riparian vegetation given the overriding influence of light in forest–agricultural boundary areas. Lastly, recent research suggests that small tropical streams may naturally have among the highest CO₂ evasion rates to the atmosphere (Raymond et al., 2013) and global agriculture is mostly expanding in tropical regions of the world (Sloan & Sayer, 2015). Hence, land use change in the tropics could lead to large annual deviations from baseline stream metabolism and amounts of CO₂ evaded from streams. Yet the magnitude and direction of this change (i.e. whether CO₂ evasion will increase or decrease) remains poorly quantified. Except from the larger NEP variation found in our agricultural study reaches, a clear pattern of NEP could not be observed from our small data set limited to the season with lower precipitation amounts. Research comparing stream metabolism between reference and agricultural areas across different biomes and seasons coupled with CO₂ evasion measurements would allow us to identify regions undergoing the largest changes in stream C cycling. This knowledge would be useful to target riparian conservation and prioritize restoration efforts.

In conclusion, forest–agricultural boundaries in headwater areas are zones of active increases in stream metabolism mainly due to higher light availability, and these changes are much more pronounced for GPP than ER. We show that shading from sparse remnant riparian vegetation influences stream metabolism, but that dense riparian canopies are key to avoid increase in the magnitude of stream metabolism. Adequate management of riparian vegetation in agricultural streams with high upstream forest cover offers great potential to achieve metabolic rates and likely support other ecosystem processes, such as nutrient cycling or secondary production, similar to forests. Our findings add to a building body of knowledge of stream metabolism in underrepresented biomes and contribute to the understanding of the within–biome variability of headwater C processing and the role of tropical streams in the global C cycle.

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Tables

Table 1.1. Characteristics of study reaches (mean \pm 1 SD). Riparian = type of riparian vegetation: fully forested (FF); isolated trees (IT); isolated trees with woody understory (ITU); herbaceous (HR). AGLC = proportion of agricultural land cover within study reach drainage area, PAR = photosynthetically active radiation, T = water temperature, D_{50} = median particle size, Q = discharge, KO_2 = reaeration coefficient, SC = specific conductance, DIN = dissolved inorganic nitrogen, SRP = soluble reactive phosphorus, Chl- a = chlorophyll a , AFDM = periphyton ash free dry mass, CPOM = coarse particulate organic matter cover, BDL = below detection limit.

| Study reach | | 1For | 2For | 3For | 1Ag | 2Ag | 3Ag | 4Ag | 5Ag | 6Ag |
|---------------------------------|--|-------------------|-------------------|-------------------|-------------------|-------------------|-------------------|--------------------|-------------------|-------------------|
| Stream order | | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 |
| Riparian | | FF | FF | FF | HR | IT | HR | IT | ITU | HR |
| AGLC | (%) | 0 | 0 | 0 | 4.2 | 3.7 | 10.5 | 11.7 | 0.1 | 7.3 |
| Canopy cover | (%) | 91 | 93 | 89 | 26 | 52 | 12 | 46 | 76 | 15 |
| PAR | (mol m ⁻² d ⁻¹) | 0.4 \pm 0.1 | 0.5 \pm 0.4 | 0.9 \pm 0.7 | 27.2 \pm 0.5 | 12.7 \pm 8.1 | 23.5 \pm 1.4 | 5.6 \pm 2.4 | 1.9 \pm 1.1 | 36.2 \pm 5.2 |
| Slope | (%) | 7 | 11 | 13 | 10 | 10 | 4 | 2 | 8 | 5 |
| T | (°C) | 20.4 \pm 0.2 | 20.5 \pm 0.2 | 21.2 \pm 0.2 | 20.4 \pm 0.3 | 19.9 \pm 0.1 | 21.7 \pm 0.4 | 22.2 \pm 0.3 | 20.7 \pm 0.1 | 22.1 \pm 0.3 |
| D_{50} | (mm) | 22.6 | 11 | 32 | 22.6 | 9.5 | 22.6 | 19.3 | 22.6 | 11 |
| Length | (m) | 65 | 90 | 75 | 90 | 75 | 76 | 70 | 78 | 80 |
| Width | (cm) | 193 \pm 70 | 135 \pm 47 | 80 \pm 18 | 153 \pm 26 | 97 \pm 16 | 94 \pm 37 | 127 \pm 31 | 169 \pm 44 | 125 \pm 57 |
| Depth | (cm) | 8.3 | 6.4 | 5.1 | 7.1 | 6.2 | 5.5 | 5.1 | 6.8 | 4.2 |
| Q | (L s ⁻¹) | 16.8 | 3.7 | 2.7 | 28.4 | 2.3 | 4.2 | 1.8 | 4.9 | 7.9 |
| Velocity | (m s ⁻¹) | 0.1 | 0.03 | 0.02 | 0.1 | 0.01 | 0.04 | 0.03 | 0.07 | 0.1 |
| KO_2 | (d ⁻¹) | 298 | 127 ^a | 100 ^a | 324 | 52 | 82 | 74 ^a | 242 | 268 |
| SC | (μ S cm ⁻¹) | 204 | 198 | 167 | 199 | 195 | 194 | 145 | 200 | 186 |
| pH | | 8 | 7.9 | 7.8 | 8.1 | 7.9 | 7.8 | 8 | 7.9 | 8.2 |
| NO ₃ ⁻ -N | (mg L ⁻¹) | 0.1 | BDL | 0.13 | 0.21 | 0.1 | 0.11 | 0.12 | 0.16 | 0.13 |
| NH ₄ ⁺ -N | (mg L ⁻¹) | BDL | BDL | BDL | 0.1 | BDL | 0.1 | BDL | BDL | BDL |
| DIN | (mg L ⁻¹) | 0.1 | BDL | 0.13 | 0.31 | 0.1 | 0.21 | 0.12 | 0.16 | 0.13 |
| SRP | (mg L ⁻¹) | 0.2 | 0.2 | 0.1 | 0.25 | 0.2 | 0.1 | 0.1 | 0.1 | 0.25 |
| Organic matter standing stocks | | | | | | | | | | |
| Chl- a | (mg m ⁻²) | 3.7 \pm 2.6 | 4.0 \pm 4.0 | 2.3 \pm 3.1 | 4.9 \pm 2.6 | 4.1 \pm 2.4 | 4.8 \pm 3.3 | 9.2 \pm 7.9 | 8.2 \pm 5.2 | 4.9 \pm 2.8 |
| AFDM | (g m ⁻²) | 7.4 \pm 2.8 | 10.0 \pm 4.2 | 9.5 \pm 4.2 | 18.6 \pm 6.3 | 19.8 \pm 7.7 | 17.2 \pm 9.6 | 25.2 \pm 12.8 | 12 \pm 6.3 | 24.1 \pm 7.9 |
| CPOM cover | (%) | 18 | 25 | 36 | 7 | 28 | 40 | 9 | 16 | 2 |

^a Indicates sites with no field measurements of reaeration where we made estimates using the equation of a polynomial relationship between KO_2 and Q in the sites with both measured variables.

Table 1.2. Loadings of principal component analysis of explanatory variables of stream metabolism across nine study reaches. PC = principal component. See table 1 for abbreviations.

| | PC1 | PC2 |
|------------------------|-------|-------|
| Variance explained (%) | 47.0 | 21.9 |
| Canopy cover | 0.55 | |
| T | -0.27 | 0.60 |
| PAR | -0.56 | |
| SRP | -0.35 | -0.66 |
| DIN | -0.30 | 0.44 |
| CPOM | 0.32 | |

Table 1.3. Significant Spearman's rank correlation between metabolic parameters (GPP = gross primary production, ER = ecosystem respiration, NEP = net ecosystem production, P/R = ratio of GPP to ER) and environmental variables. NS = not significant. In parentheses $p \leq 0.05$. Abbreviations are shown in table 1.

| | GPP | ER | NEP | P/R |
|---------------------------------|--------------|-------------|--------------|--------------|
| PAR | 0.51 (0.003) | NS | 0.52 (0.002) | 0.7 (<0.001) |
| Canopy cover | NS | NS | NS | -0.65 (0.05) |
| Chl- <i>a</i> | 0.76 (0.02) | NS | NS | NS |
| AFDM | 0.68 (0.04) | NS | NS | 0.8 (0.009) |
| CPOM | -0.68 (0.04) | NS | NS | -0.7 (0.04) |
| AGLC | NS | NS | NS | NS |
| NO ₃ ⁻ -N | 0.69 (0.04) | NS | NS | NS |
| T | NS | 0.43 (0.02) | NS | NS |

Table. 1.4. Summaries of linear mixed effect models. GPP = gross primary production, ER = ecosystem respiration, PC = principal component.

| GPP | | | | | |
|------------------|----------|------|----|----------|----------|
| Variable | Estimate | SE | DF | <i>t</i> | <i>p</i> |
| <i>Intercept</i> | 0.47 | 0.1 | 21 | 4.19 | <0.001 |
| PC1 | -0.08 | 0.03 | 21 | -2.69 | <0.01 |
| ER | | | | | |
| <i>Intercept</i> | 0.66 | 0.12 | 20 | 5.15 | <0.001 |
| GPP | 0.20 | 0.07 | 20 | 2.74 | 0.01 |
| PC2 | 0.03 | 0.01 | 20 | 2.63 | 0.02 |

Figures

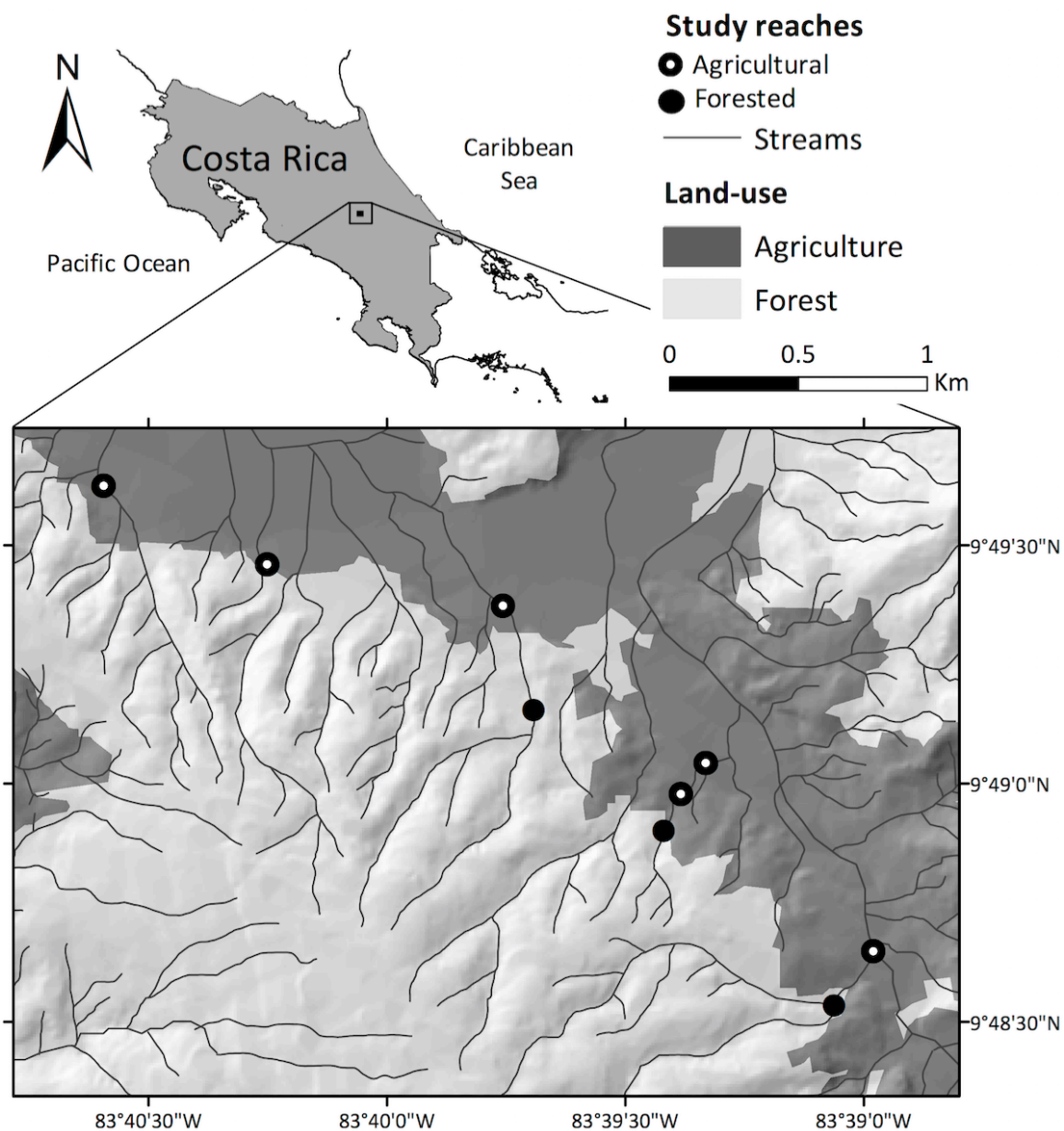


Fig. 1.1. Location of study area in the Volcánica Central Talamanca Biological Corridor, central Costa Rica. Circles indicate the downstream end of each study reach, showing three forested and six agricultural study reaches distributed in six headwater streams.

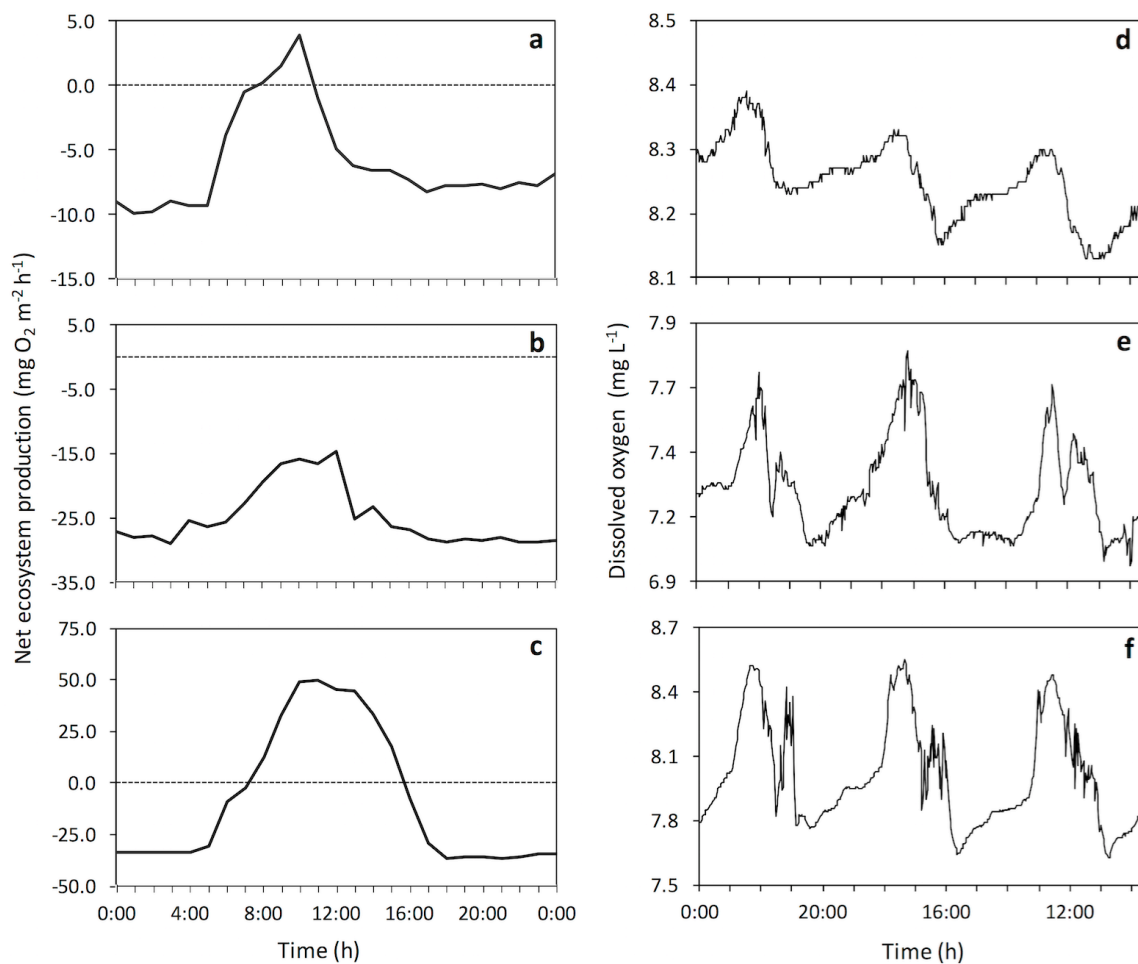


Fig.1.2. Example of daily net ecosystem production and three diel curves of dissolved oxygen at three study reaches. Study Reach *1For*: GPP = 0.06 and ER = 0.21 g O₂ m⁻² day⁻¹ (a, d); study Reach *2Ag* GPP = 0.41 and ER = 0.67 g O₂ m⁻² day⁻¹ (b, e); study Reach *6Ag*: GPP = 1.07 and ER = 0.83 g O₂ m⁻² day⁻¹ (c, f).

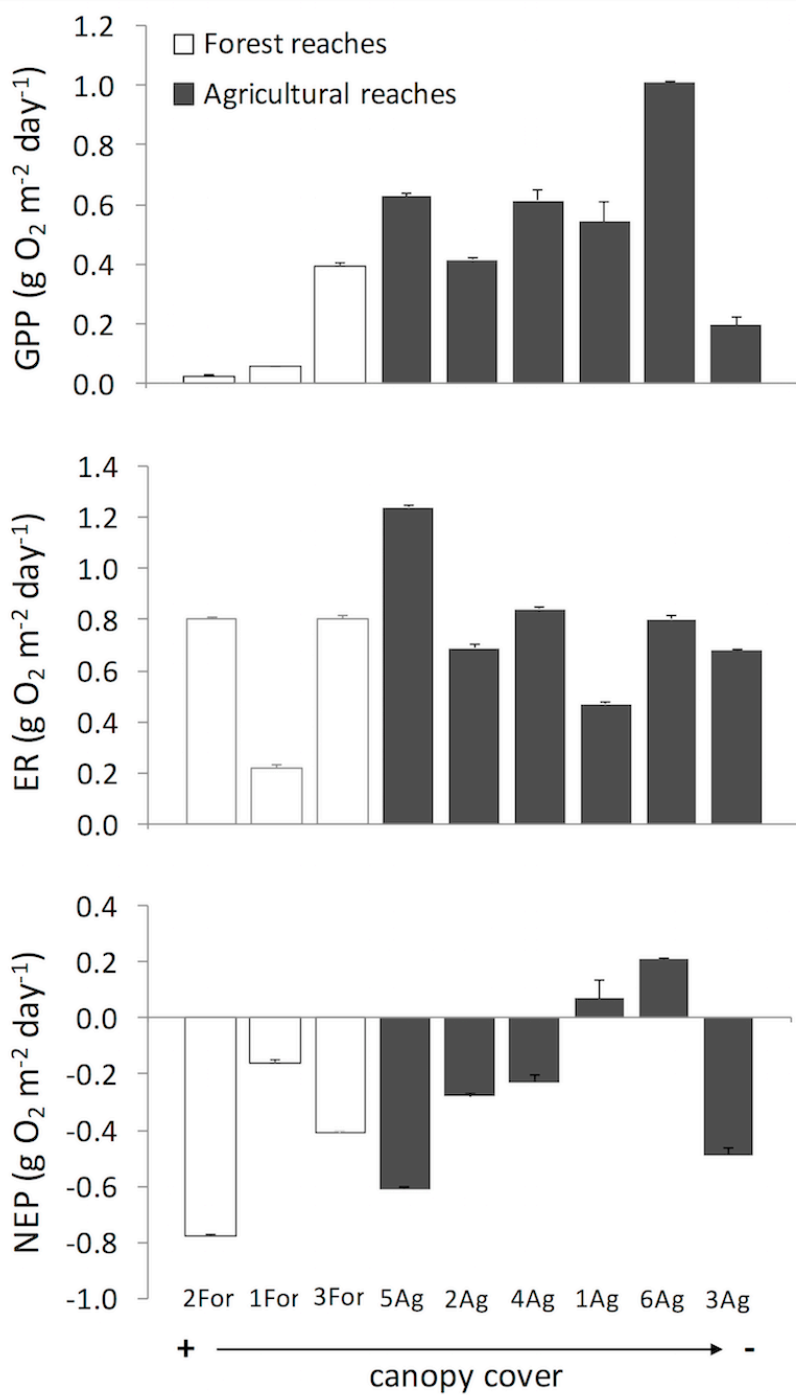


Fig. 1.3. Mean daily stream metabolism parameters (± 1 SE) in nine study reaches in a humid tropical watershed, central Costa Rica. Gross primary production (GPP) (a), ecosystem respiration (ER) (b), and net ecosystem production (NEP) (c). The x-axis indicates each site.

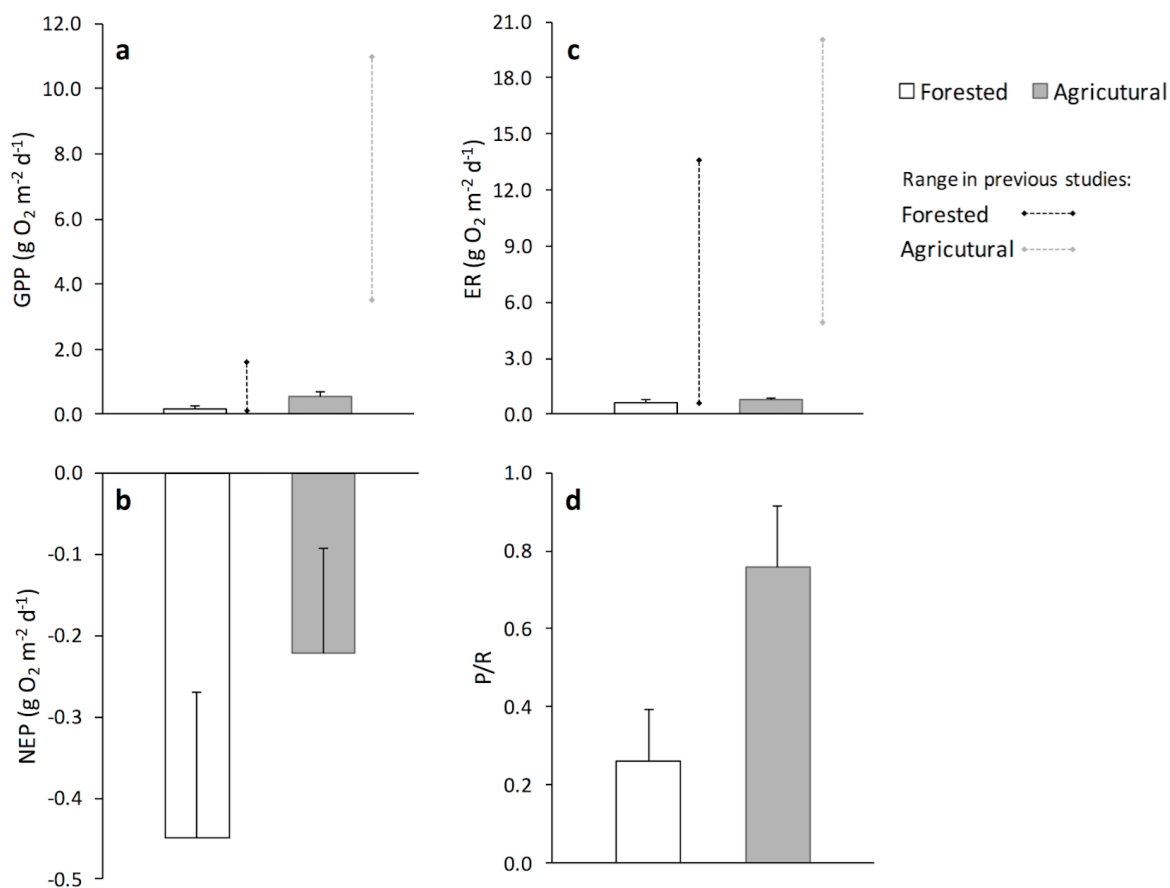


Fig. 1.4. Mean stream metabolic parameters (± 1 SE) in forested and agricultural study reaches. Gross primary production (GPP) (a); net ecosystem production (NEP) (b); ecosystem respiration (ER) (c); ratio of GPP to ER (P/R) (d). Dotted lines next to GPP and ER bars indicate the range of metabolic rates previously found by other studies of humid tropical headwater streams draining forests or croplands.

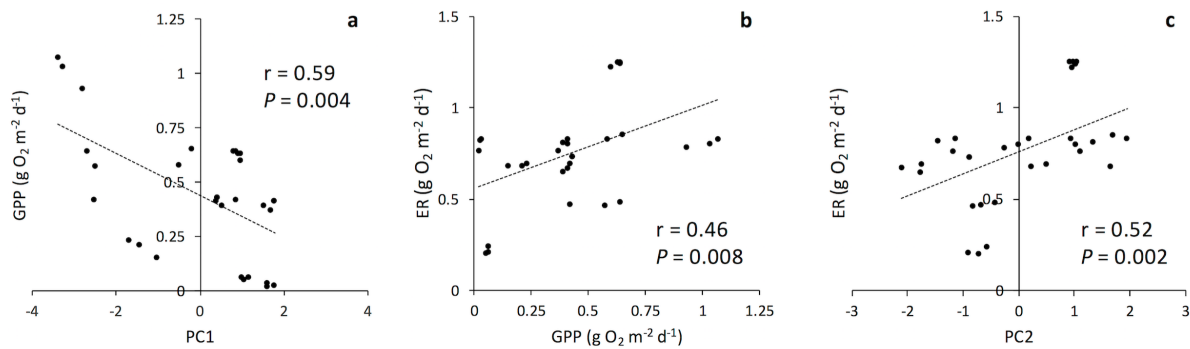


Fig. 1.5. Relationship between metabolic parameters and variables included in the best statistical models. Gross primary production (GPP) (a); ecosystem respiration (ER) (b, c); principal component (PC).

Chapter 2: Stream metabolic responses to agricultural conversion differ across biomes and food production systems

Abstract

Agricultural land use has modified the rates at which streams produce and consume organic carbon through gross primary production (GPP) and ecosystem respiration (ER) (i.e. stream metabolism). Syntheses of land use change impacts on stream metabolism have mainly assessed the combined effect of multiple anthropogenic land uses and have not tested whether metabolic rates differ across biomes or between types of agricultural systems. We conducted a global meta-analysis of agricultural influences on stream metabolism using a database including 195 streams found in the primary literature. We asked the following questions: does stream metabolism in biomes with contrasting native riparian vegetation types (i.e. forested vs. grasses/shrubs) respond differently to agriculture? And, does the magnitude of GPP and ER differ between croplands and pastures? We found that the proportion of agricultural land use in a watershed leads to GPP increases in forested biomes and to slight GPP decreases in biomes dominated by shorter riparian vegetation, mainly due to differences in how agriculture modifies the light regime with each riparian vegetation type. Across biomes, light is the most consistent predictor of GPP and leads to larger GPP increases in biomes with short versus forested riparian vegetation. ER was lower in croplands than in pastures indicating that the magnitude of agricultural effects varies between systems. This study improves our understanding of agricultural land use on freshwater carbon dynamics globally by recognizing distinct contributions of biomes and agricultural types, and informs the trade-offs between global food production and stream ecosystem function.

Introduction

Food production dominates global land use change and is the leading cause of stream ecosystems impairment (Foley et al. 2011; Carpenter et al. 2011). Agriculture alters the energy base of streams by modifying the timing and magnitude of organic carbon processing (i.e. stream metabolism) via gross primary production (GPP) and ecosystem respiration (ER) (Bernot et al. 2010; Griffiths et al. 2013). Stream metabolism is typically higher in agricultural streams than in those with little or no human influence (termed *reference* streams

hereafter), and GPP tends to increase more than ER (Bernot et al. 2010). Because ER generally greatly exceeds GPP, agricultural streams remain net consumers of energy and sources of atmospheric carbon dioxide (Hoellein et al. 2013; Hotchkiss et al. 2015). Agricultural stream ecosystems also produce more in-stream carbon (autochthonous) compared to reference streams, where a large fraction of organic carbon sources may be originated in terrestrial systems (allochthonous) (Hagen et al. 2010). Changes in basal resources have critical implications on stream ecosystems as these largely alter food web and ecosystem process (Finlay, 2011; Marcarelli et al. 2011). Furthermore, given the significant role of stream ecosystems in global carbon fluxes (Cole et al. 2007; Raymond et al. 2013), changes in agricultural stream metabolism may alter the carbon cycle globally (Carpenter et al. 2011; Demars et al. 2016).

Over the past two decades, a mechanistic understanding of agricultural influences on stream metabolism has derived disproportionately from forested temperate and subtropical regions (Tank et al. 2010; Staehr et al. 2012). In addition, syntheses of anthropogenic activities on stream metabolism have mainly investigated the aggregated effects of multiple land use types, such as urban, logging, agriculture or mining (Young et al. 2008; Finlay 2011; Hoellein et al. 2013; but see Bernot et al. 2010; Hagen et al. 2010), despite the fact that human activities can differently influence ecosystem processes (Allan 2004). Thus, we still lack a synthetic view of stream metabolic changes resulting from agriculture across world biomes and among different forms of agriculture.

Agriculture-induced changes in stream metabolism can result from higher solar irradiance and nutrient availability, elevated water temperature, and changes in hydrology, channel geomorphology and organic matter (Bernot et al. 2010; Griffiths et al. 2013; Yates et al. 2013). Yet, among these, light exerts a primary control on metabolic rates directly by driving GPP and indirectly by increasing autotrophic respiration (AR) or water temperature, which can accelerate overall metabolic activity (Yvon-Durocher et al. 2010; Finlay 2011; Hoellein et al. 2013).

The mechanism leading to higher light availability in agricultural streams is the reduction or removal of riparian vegetation (McTammany et al. 2007). However, riparian vegetation characteristics naturally vary among terrestrial biomes leading to differences in stream light regimes and in the relative importance of ecosystem carbon sources (Minshall 1978; Hill

1996; Webster and Meyer 1997; Hagen et al. 2010). Specifically, stream ecosystems located in forested terrestrial biomes tend to be strongly light limited and allochthonous carbon by far exceed autochthonous production (Lamberti and Steinman 1997). Conversely, light availability and autotrophic carbon production are generally high in biomes where riparian areas are dominated by shorter vegetation, such as shrubs or grasses (Wiley et al. 1990). Previous research has shown that light influences autotrophic community composition because different functional groups have distinct responses to light (Steinman et al. 1992; Hillebrand 2005). Thus, if autotrophic communities in reference streams are adapted to thrive under specific light conditions, metabolic responses to agriculture could differ between streams in biomes with naturally open riparian canopies (OB) and streams located in forested biomes (FB) (Fig. 2.1).

Agricultural land can be divided into two major types - croplands and rangelands or areas covered with human-made pastures for rearing livestock (FAO 2015). Although these categories are broad, factors influencing stream metabolism can uniquely associate with each agricultural type (Yates et al. 2014). For example, the widespread use of agrochemicals such as pesticides and herbicides which affect stream function is highly common in intensive row crop systems (Carvalho 2006; Schäfer et al. 2007). Also, croplands have higher erosion rates and water sediment concentrations than pastures (Pimentel and Kounang 1998; Meador and Goldstein 2003; Zaines et al. 2004), and sediments can also decrease stream metabolism through several pathways, such as algae scouring or by filling streambed interstitial space (Uehlinger and Naegli 1998; Hancock 2002). Yet, only few studies have explicitly addressed whether differences in stream metabolism can be observed between these two agricultural types (e.g. Young and Huryn 1999; Yates et al. 2013, 2014).

To explore differences in SM across biomes with contrasting riparian vegetation (i.e. OB and FB) and between the two major types of agriculture, we built a dataset from published peer-reviewed literature including 195 streams from various world biomes, spanning a wide latitudinal range, and located in watershed ranging from 0% to 100% agriculture cover. Our overarching goal was to provide a global synthesis of SM in agricultural contexts. In particular, we set out to answer the following questions: 1) Does stream metabolism in biomes with original open versus closed riparian vegetation respond differently to agriculture; and, 2) do metabolic rates differ between croplands and pasture systems? Our findings have

implications for understanding agricultural effects on the energy base of stream ecosystems and in the contribution of streams to the global carbon cycle.

Methods

Data collection

Between May and June 2016, we searched the peer-reviewed literature for studies of stream metabolism in the Web of Science, BIOSIS, and Google Scholar. We used combinations of the following search terms: stream metabolism, whole-stream metabolism, agriculture, land-use change, net ecosystem metabolism, agricultural stream, stream carbon, gross primary production. From this initial query, we screened 104 journal articles. From these papers, we selected 45 studies that met our selection criteria. Our criteria were as follows: studies including 1st-3rd Strahler order streams that measured stream metabolism using the single or two-station open-water method and studies that collected data during stable summertime flows or in late spring when summers were associated with high levels of precipitation. We excluded streams draining watersheds with > 5% urban land use cover or with direct urban influences, such as water inputs from treatment plants or sewage or where urban establishments were adjacent to streams. We also excluded streams with > 5% cover of logging areas within their drainages, channelized streams with paved streambeds or alterations preventing hyporheic exchange, and streams influenced by aquaculture or mining activities. We initially intended to only include studies with field measurements of reaeration but doing so would have drastically reduced our data, so we also included studies with modeled rates of reaeration.

We contacted authors to request for raw data, and built a data base with the variables of interest or a subset of these when not all were available. (Table 2.1). Eight studies reported raw data and we successfully established contact with 13 authors who provided raw data for 16 studies. The final data base was built with 24 studies and including 195 streams (Table A1).

Database and data categorization

When streams had multiple observations of a given variable, we averaged all measurements to obtain a single value per stream. Prior to analysis, we categorized streams in three distinct ways:

- a. Reference and agricultural streams: With the goal of documenting reference and agricultural conditions accurately, we initially explored the relationship between metabolic parameters and the proportion of agriculture cover in the watershed to inspect for potential inflection points. Since we did not find any clear patterns we used an arbitrary categorization approach similar to other previous studies (e.g. Finlay 2011). Specifically, we assigned streams to the reference category when agriculture cover within their drainage was $\leq 10\%$ ($n = 99$) and to the agricultural category when agriculture cover was $> 10\%$ ($n = 96$) (Table A2). Near 60% of streams categorized as reference had no agriculture cover and 30% had less than 5% agriculture cover. The risk of this approach could be to classify streams as reference systems with fractions of agriculture cover $< 10\%$ but with agricultural activities happening adjacent to streams, as this could modify key proximal drivers of stream metabolism such as light. Yet, we think that 90% of the reference stream data set having maximum 5% agriculture cover provided a good representation of reference conditions.
- b. Biome type and group: To standardize terms describing each stream's biome, we used the World Wildlife fund (WWF) terrestrial world biome categories proposed by Olson et al. (2001). We used ArcGIS (ESRI, USA) to intersect each study's GPS coordinates with the layer of Terrestrial Ecoregions of the World (WWF, 2004) and confirmed that the assigned category was accurate based on study site descriptions or by asking authors directly. Only 2% of streams had to be reassigned to a different biome category. We then split all biomes into two groups based on the type of dominant vegetation cover. Specifically, we divided biomes into two groups: forested biomes (FB) and open biomes (OB) (Table 2.2). Our grouping criterion was the likelihood of a reference stream to have either abundant or limited light as a result of riparian vegetation structural characteristics. Specifically, we expected FB to be shaded by dense, tall tree stands and OB to have more available light with riparian vegetation being dominated by shrubs, grasses or sparse trees. We tested whether the light environment, specifically PAR, differed between FB and OB

and found significant difference between the two groups, with PAR being lower in FB than in OP (Wilcoxon sum rank test, $p < 0.0001$) (Table 2.2).

- c. Streams draining row-crop or pastures systems: In order to explore differences between agricultural system types, we selected all streams in watersheds where agricultural land use was largely (i.e. $> 80\%$) or completely dominated by either row-crops or pastures. Since watersheds with mixed agricultural land uses are common, the final dataset for this comparison consisted of 33 streams in row-crops and 74 streams in pastures. We define pastures as any natural or human-made grassland used to raise livestock.

Statistical analyses

To test whether metabolic rates in OB were higher than in FB, we used the Wilcoxon Rank Sum test. When streams had multiple observations of a given variable, we averaged all measurements to obtain a single value per stream. To test the hypotheses that stream metabolic responses to agricultural land use differ between FB and OB, we used linear mixed effect models (*nlme* R package for linear mixed effect modelling, R Development Core Team 2016; Zuur et al. 2009). We transformed dependent and independent variables to achieve normality and used the transformed dataset to build the statistical models of GPP and ER (Table 2.1). The full model of GPP included PAR, Ag, DIN, SRP and their interaction with biome group as fixed factors. The full model of ER included GPP, Ag, Temp, Q , DIN and SRP, and their interaction with biome type as fixed effects. Both models included *study* as a random effect to account for inter study variation (Mengersen et al. 2013). We fitted models using the restricted maximum likelihood (REML) approach and visually inspected model diagnostic plots (Zuur et al. 2009). To meet the assumptions of the ER model, we included Ag as a variance covariate using the *VarExp* function. We found the simplest fixed effect structure by comparing nested models using the maximum likelihood ratio test (Zuur et al. 2009). We then refitted the selected model with the REML and re-inspected diagnostic plots. We used the marginal r^2 and conditional r^2 to estimate the variance explained by the model's fixed factors alone and by the fixed and random factors jointly, respectively (*MuMIn* package, R development core team 2016). The dataset including complete cases of variables in the full model of GPP consisted of 89 observations. Since neither DIN nor SRP were included in the model's best fixed structure, we ran the full model of GPP again using a larger data set

including complete cases of PAR and Ag ($n = 124$). To explore bivariate correlations between and among metabolic parameters and environmental variables, we used Pearson's correlation analyses with the set of transformed variables.

To test whether metabolic parameters and environmental variables differed between row-crop and pasture agricultural systems, we used the Wilcoxon rank sum test for variables with equal variance and the Kolmogorov-Smirnov test for variables with unequal variance. We also explored for bivariate associations in each agricultural type with Pearson's correlation using the set of transformed variables. All statistical analyses were performed with R statistical software (R development Core Team 2016).

Results

Metabolism in reference systems

We found metabolism studies of reference streams in nine of the 12 world biomes where streams are present ($n = 98$) (Table 2.2). Unrepresented biomes included tropical and subtropical dry broadleaf forests, tropical and subtropical coniferous forests, and tundra. Metabolism studies were most abundant in temperate broadleaf and mixed forest, followed by tropical and subtropical moist broadleaf forest. Boreal forest and montane grasslands and shrublands were the biomes with fewer studied streams. GPP across all biomes ranged from $0.0 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ to $13.6 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$, and ER ranged from $0.2 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ to $25.46 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ (Table 2.2). GPP and ER in reference streams were lower in forested biomes (FB) than in open biomes (OB) (Wilcoxon sum rank test, $p < 0.0001$ and $p = 0.01$). Particularly, GPP in FB ranged from $0.004 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ to $3.11 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ and ER from $0.2 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ to $14.6 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$, while GPP in OB ranged from 0.0 to $13.6 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ and ER ranged from $0.78 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ to $25.46 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ (Fig. 2.2).

Metabolism in agricultural systems

We found six biomes with both reference and agricultural streams studies. Three of these were FB and three were OB (Table 2.2). In general, the magnitude of metabolic rates in FB and OB became more similar with agriculture. Comparing metabolic rates between reference and agricultural systems, both GPP and ER increased in FB and decreased OB (Fig. 2.2). In reference streams, median GPP was 87% higher in OB than in FB; with agriculture, this

difference decreased to 31%. Specifically, in FB, GPP increased from $0.24 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ to $1.16 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ from reference to agriculture, and in OB slightly decreased from $1.8 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ to $1.67 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ (Fig. 2.2A, D). Median ER in FB increased from $3.03 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ in reference streams to $4.25 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ in agricultural streams. Conversely, median ER in OB decreased from $5.55 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ to $3.35 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ from reference to agriculture (Fig. 2.2B, E). NEP across systems was negative and closer to zero in agricultural streams compared to reference systems in both FB and OB. The largest NEP change was observed in OB where median rates shifted from $-3.75 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ in reference to $-1.58 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ in agricultural streams (Fig. 2.2C, F).

Drivers of stream metabolism

The statistical model of GPP showed that variation was explained by PAR, Ag and the interaction of these two variables with biome group (i.e. FB or OB) (Table 2.3). Significant interaction terms indicate that both the effect of PAR and Ag over GPP differed between FB and OB (Fig. 2.3). We found significant correlations between GPP and PAR in FB and OB ($r = 0.63, p < 0.001$ in both cases), and between GPP and Ag in FB ($r = 0.51, p < 0.001$). GPP in FB was also positively associated with DIN ($r = 0.31, p = 0.003$), but DIN did not have a significant effect in the models of GPP.

The final model of ER included GPP, DIN and Q as explanatory variables with no significant interaction terms (Table 2.3). ER was positively correlated with GPP in FB ($r = 0.39, p < 0.001$) and OB ($r = 0.42, p < 0.001$) (Fig. 2.4). ER was also correlated with Ag but the direction of this relationship differed between biome categories, with ER being positively correlated with Ag in FB ($r = 0.25, p = 0.005$) and negatively correlated in OB ($r = 0.26, p = 0.04$). Overall, the model of GPP explained more variation than the ER model. Marginal and conditional r^2 in the former were 0.59 and 0.61, and 0.06 and 0.22 in the latter (Table 2.3).

Environmental characteristics and metabolism in row-crop and pasture streams

In general, the weightings of environmental factors correlating with SM were similar in streams draining row-crops and pastures (Table 2.4). Average Ag was near 40% in both land uses and canopy cover was ~24%. Mean PAR was higher in row-crop than pasture streams but this difference was not statistically significant at the $p = 0.05$ level (Wilcoxon rank sum

test, $p = 0.06$). Pastures had larger drainage areas than row-crop systems (Wilcoxon rank sum test, $p = 0.007$) and D_{50} was larger in pasture than in row-crop streams (Wilcoxon rank sum test, $p = 0.02$). Channel width also statistically differed between the two agricultural types (Kolmogorov-Smirnov test, $p = 0.02$) with pasture streams being in average 1 m wider than streams draining row-crops (Table 2.4).

Average GPP in row-crop and pasture streams was $2.26 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ and $1.17 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$, but were not statistically different (Fig. 2.5A). In both row-crop and pasture areas GPP was correlated with PAR ($r = 0.46, p = 0.03$ and $r = 0.81, p < 0.0001$), Ag ($r = 0.59, p = 0.0003$ and $r = 0.32, p = 0.009$) and canopy cover ($r = -0.47, p = 0.030$ and $r = 0.63, p = 0.004$). GPP and ER were also associated in both row-crop ($r = 0.62, P = 0.001$) and pasture systems ($r = 0.40, P < 0.001$). We found significant differences in ER between agricultural types (Wilcoxon rank sum test, $p = 0.0001$). Average ER in row-crop streams was $3.29 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ and in pastures was $5.29 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$. We only found significant correlations between ER and other environmental variables in streams draining row-crops. In particular, ER was associated with PAR ($r = 0.40, p = 0.02$), Ag ($r = 0.44, p = 0.01$) and DIN ($r = 0.45, p < 0.0001$). Stream NEP was less negative in croplands than pastures ($p < 0.0001$) (Fig. 2.5C).

Discussion

Our dataset represents the most detailed compilation of stream metabolism studies in agricultural systems to date and provides insights into the changes in stream functioning with land conversion to agriculture. We show that stream metabolic responses to agriculture depend largely on reference riparian vegetation and that food production systems exert different influences on stream metabolism. Our results further our understanding of global changes in stream C processing and stream ecosystem basal resources by highlight the importance of accounting for the different influences of biomes and food production systems.

Light as a grouping variable in streams

Our results show that grouping streams by riparian vegetation characteristics is a direct way to classify agricultural effects on stream functioning during summer periods. We note that grouping biomes based on expected riparian vegetation characteristics assumes that FB will have lower light availability than OB, but shrub and herbaceous riparian species in OB can

also significantly shade streams (Beschta 1997). Still, terrestrial biomes represent a coarse scale; thus, it is reasonable to expect lower light availability in FB than in OB (Dodds et al. 2015). The lower reference GPP in FB than OB found in this study is supported by previous research showing that forest streams tend to have lower GPP than desert or tundra streams due to the large influences of climate over terrestrial vegetation (Lamberti and Steinman 1997; Webster and Meyer 1997). Explicitly separating stream metabolism into FB and OB has potential to benefit a variety of activities such as assessments of stream ecosystem condition or modelling efforts of stream metabolism and global carbon cycling (Battin et al. 2008; Young et al. 2008).

Gross primary production in agricultural areas

Our findings provide evidence that fundamental differences between FB and OB riparian vegetation translate into distinct metabolic responses to agriculture (Table 2.3; Fig. 2.3). Unlike in OB where streams naturally have high levels of irradiance, agriculture greatly modifies stream light regimes in FB by significantly increasing light through reductions in riparian vegetation. Accordingly, in this study, *Ag* was not significantly associated with PAR in OB. Thus, the outcome that *Ag* only increased GPP in FB was likely the result of stream autotrophic communities being released from light limitation (Hill et al. 1995; Bernot et al. 2010). In general, the effect of agricultural land use can be difficult to detect as positive and negative effects of different controls of GPP, can reflect in no changes in metabolic rates (Hall 2016). We expect drivers to have these opposite effects on GPP in both OB and FB; yet, the fact that GPP slightly decreased with *Ag* in OB may be attributed to stream autotrophs in OB not undergoing the resource boost that light represents for FB in agricultural areas. Hence, with no light limitation, the effect of other drivers that reduce GPP, such as sediments lowering streambed irradiance, could become more apparent in OB than FB (Young and Huryn 1999; Young et al. 2008). Overall, the only variable consistently predicting increase in GPP was PAR.

The fact that PAR in OB regularly reached higher levels than FB (Fig. 2.3) likely explains why PAR had a stronger effect on GPP in OB than in the FB. We reason there are two main factors operating at different scales that can determine why even with similar or no riparian canopy cover, streams in OB may receive more light than FB. Locally, differences in riparian

vegetation structure can lead to contrasting light regimes because trees block a larger proportion of incoming radiation and shade larger areas than grasses and shrubs due to their taller stature and more extensive canopies (Beschta 1997). At larger scales, difference in climate and topography could drive differences in PAR between OB and FB; specifically, forested headwaters often occur in mountainous terrain where precipitation amounts are high compared to deserts, prairies or savannas where land is generally flatter and receives less rain (Leopold et al. 1964; Minshall et al. 1985). These differences strongly influence stream geomorphology, the degree to which topography, banks and riparian vegetation shade streams, and ultimately, metabolic rates (Church 2002; Bott et al. 2006; Dodds et al. 2015). Given that light is a key variable influencing autotrophic community structure and function, differences in light-adaptations between OB and FB autotrophic communities could likely be expressed as higher GPP in OB than FB (Steinman et al. 1992; Roberts et al. 2004). Autotrophs in OB could have functional advantages over those in FB because algal communities in reference OB are generally light-adapted, whereas communities in FB are largely made up by shade-adapted species (Minshall 1978; Hill 1996). For example, with increases in light stream autotrophs in FB could be more prone to experience self-shading than in OB due to the prevalence of smaller versus larger algal growth forms, respectively (Boston and Hill 1991; Hill 1996; Hillebrand 2005). Also, compared to OB, shade-adapted autotrophs in FB could reach light saturation at lower light levels (Mulholland et al. 2001; Bott et al. 2006), or experience photoinhibition due to a potential lack of accessory photoprotective pigments (Boston and Hill 1991; Hill et al. 1995). Given that autotrophic communities are not static, increases in light in FB may eventually lead to communities being dominated by light-adapted species (Bunn et al. 1999; Hagen et al. 2010). Yet, the fact that autotrophic communities in OB are less likely to undergo large changes in light adaptation may explain the different effect of PAR on GPP in OB and FB.

Overall, the outcome that PAR and A_g predicted GPP is in agreement with a large body of research, largely undertaken during summer periods, and can be attributed to the governing effect of PAR over GPP and that A_g provides an integrative measure of agricultural influences (Mulholland et al. 2001; Allan 2004; Bernot et al. 2010; Hoellein et al. 2013; Yates et al. 2013). However, while PAR continues to stand out as a consistent driver of GPP across biomes, it is clear that A_g may not be as strong as a predictor of GPP in OB as it is in FB. We

note that the patterns of GPP may vary within and between biome types at larger temporal scales such as seasonal, annual or inter-annual, stressing the critical importance of performing metabolic measurements spanning longer time frames (Roley et al. 2014; Hall, 2016). The fact that neither DIN or SRP predicted GPP is not surprising. Previous studies have attributed this lack of association to water column nutrients not representing demand or relevant nutrient benthic processes (Dodds 2003; Hoellein et al. 2013), and to the fact that nutrient concentrations in agricultural streams will hardly limit GPP (Carpenter et al. 1998).

Ecosystem respiration in agricultural areas

Our results indicate that ER is not significantly modified by agricultural land use nor does it differ across terrestrial biomes when these are grouped into OB and FB. However, the overall predictive power of the ER model was low. This could have been in part because the model did not include potential drivers like dissolved organic matter (Maseke et al. 2016; Fuß et al. 2017) because they are reported in only a few studies. In addition, estimates of ER can have high uncertainty (McCutchan et al. 1998; Hotchkiss and Hall 2014) and ER is likely less affected by land use because heterotrophs are less influenced by light and may receive constant inputs of allochthonous C (Dodds 2006; Finlay 2011). Accordingly, past research has shown mixed results when assessing agricultural effects over ER. Some studies have found agriculture to increase ER due to increase in GPP or nutrients (Burrell et al. 2013; Yates et al. 2013), to decrease ER due to drops in C rich terrestrial organic matter inputs (Young and Huryn 1999), or have found ER to not differ between reference and agricultural streams or across gradients of land use intensity (McTammany et al. 2007). Thus, we argue that the relevance of agricultural influences on ER likely relies more on the relative contributions of C sources supporting heterotrophic versus autotrophic respiration (Hagen et al. 2010; Doods 2006), rather than on the absolute magnitude of ER.

Potential implications of agriculture on autotrophic C availability

Increase in ER driven by GPP mainly result from higher autotrophic respiration (Fig. 2.4). Estimates of the proportion of GPP immediately respired by autotrophs and their closely associated heterotrophs (AR_f after Hall and Beaulieu 2013) can be used to roughly calculate the amount of autotrophic C available for consumers. Based on a value of $AR_f = 0.56$

obtained by averaging values found in a literature search and this study (Table A3), our results indicate that agriculture potentially increases autotrophic C availability in OB from $0.38 \text{ g C m}^{-2} \text{ day}^{-1}$ to $0.45 \text{ g C m}^{-2} \text{ day}^{-1}$ (17%), and in FB from $0.06 \text{ g C m}^{-2} \text{ day}^{-1}$ to $0.26 \text{ g C m}^{-2} \text{ day}^{-1}$ (304%). Considering that OB naturally have high autotrophic production (Minshall 1978; Lamberti and Steinman 1997) and that consumers have a strong preference for autotrophic C sources (Marcarelli et al. 2011), these estimates suggest that with agriculture, streams in FB are much more vulnerable to undergo large food web modifications than OB (Finlay 2011). These values likely represent the highest levels of autotrophy occurring during the year given our focus on summer stream metabolism (Griffiths et al. 2013). Also, estimates of ARf could be overestimated due to the priming effect of organic compounds from photosynthesis on heterotrophic activity (Hall and Beaulieu 2013). Still, these results provide key insights to potential changes in basal resources and suggest that food webs in stream draining forests may be the highly threatened by agricultural land use.

Stream metabolism in croplands and pastures

We illustrate that within the broad category of land agricultural land use, stream metabolism may be further understood by differentiating the effects of croplands and pastures. These findings represent a first step towards understanding stream metabolism across food production systems because global variation between and among systems is likely high due to a wide range of potential influences from climate, management practices, and crop types and livestock species.

We attribute having found similar GPP in croplands and pastures to the fact that we based our comparisons on summertime streams metabolism under stable flows, and that potential controls of GPP such as PAR or nutrients did not differ between croplands and pastures (Table 2.4). Mechanisms linked to biomass loss, such as periphyton scouring by sediment, transport of unstable substrate with high velocities, or light attenuation from suspended particles, typically occur with high flows (Biggs 1996). Also, even though pesticides can clearly lead to autotrophic biomass loss, during base flows pesticide concentrations can be below levels harmful to autotrophs (Hoagland et al. 1996). Hence, if GPP differs between agricultural types, these patterns may be more easily observed with measurement encompassing several seasons. In addition, we note that our inferences are based on a small

sample size, which could also potentially prevent us from detecting different GPP patterns across agricultural types.

Given the similar GPP in croplands and pastures, ER was likely significantly lower in the former than in the latter due to differences in heterotrophic activity. Alternatively, our results could also be attributed to the larger mean drainage area in pastures than in croplands because ER correlates with watershed area (Finlay 2011). Yet we reason that differences in ER between agricultural types could be expected for the following reasons. Channelized cropland streams have low organic matter retention which could translate into low ER (Elosegi and Sabater 2012; Kominoski and Rosemond 2012). Also, watersheds dominated by crops have significantly higher land and streambank erosion rates than pastures due to differences in soil cover and riparian vegetation (Pimentel and Kounang 1998; Zaimes et al. 2004). These differences may lead to higher suspended sediment loads in croplands than in pastures (Dodds and Whiles 2004). Given that hyporheic zones can account for large fractions of ER (Fellows et al. 2001), the lower ER in croplands could be the result of high sediment inputs impacting hyporheic communities through colmation or toxicity (Brunke and Gosner 1997; Hancock 2002). Although we lack information of variables related to sediment loads, the significantly smaller D_{50} found in croplands than in pastures could indirectly support this reasoning because high sediment loads lead to finer streambed particles with higher sediment storage capacities (Dietrich et al., 1989; Madej et al., 2009). Overall, these findings suggest that differences in the magnitude of environmental impacts associated with agricultural types also translate into particular effect on stream metabolism.

Final remarks

Agricultural land use has strongly influenced stream metabolism globally. Our results inform where stream ecosystem basal resources and carbon processing rates have likely been more drastically modified across the globe. The sensitivity of FB to agricultural conversion stresses the critical importance of conserving and restoring riparian forests as a strategy to avoid drastic declines in biodiversity and ecosystem services. While our findings indicate larger changes in stream metabolism and carbon sources in FB than OB, past research has shown that agriculture can clearly influence stream structure and function in OB (Dodds et al. 2004). Thus, management practices to increase agricultural sustainability are also urgently needed in

OB and may need to focus more on improving factors leading to poor water quality such as sediment or nutrient inputs. Our findings of ER in croplands and pastures highlights the need to transition from a general to a more particular mechanistic understanding agricultural effects on stream function. Lastly, despite the important role of stream in the global carbon cycle (Raymond et al. 2013), global estimates of stream carbon fluxes have not explicitly accounted for differences in metabolism between reference and agricultural streams (Griffiths et al. 2013). This study fills a gap that can help to refine estimates of internal carbon processing in streams and the implications for the cycling of carbon globally.

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Tables

Table 2.1. Variables used for meta-analysis of global impacts of agriculture on stream metabolism.

| Variable | Id | Units | Transformation |
|-------------------------------------|-----------------|--|---------------------|
| Biomes (forested open) | FB OB | | |
| Gross primary production | GPP | g O ₂ m ⁻² day ⁻¹ | Natural log |
| Ecosystem respiration | ER | g O ₂ m ⁻² day ⁻¹ | Natural log |
| Net ecosystem production | NEP | g O ₂ m ⁻² day ⁻¹ | |
| GPP immediately respired | AR _f | % | |
| Agricultural land within drainage | Ag | % | Arcsine square root |
| Photosynthetically active radiation | PAR | mol m ⁻² day ⁻¹ | Natural log |
| Canopy cover | | % | Arcsine square root |
| Discharge | <i>Q</i> | L s ⁻¹ | Natural log |
| Channel width | | m | Natural log |
| Median particle size | D ₅₀ | mm | Natural log |
| Water temperature | Temp | Degrees Celsius | Natural log |
| Drainage area | | Km ² | Natural log |
| Dissolved inorganic nitrogen | DIN | µg N L ⁻¹ | Natural log |
| Soluble reactive phosphorus | SRP | µg P L ⁻¹ | Natural log |

Table 2.2. Average metabolic rates (\pm sd) of references sites ($< 10\%$ agriculture cover within drainage) across biomes of the world. GPP = gross primary production; ER = ecosystem respiration; PAR = photosynthetically active radiation; FB = forested biomes; OB = open biomes.

| Biome | Stream <i>n</i> | GPP g O ₂ m ⁻² day ⁻¹ | ER g O ₂ m ⁻² day ⁻¹ | PAR mol m ⁻² day ⁻¹ | Biome group |
|---|--------------------|---|--|--|----------------|
| Tropical and subtropical moist broadleaf forest* | 17 | 0.59 \pm 0.59 | 3.50 \pm 3.82 | 7.0 \pm 12.17 | FB |
| Temperate broadleaf and mixed forests* | 28 | 0.26 \pm 0.28 | 5.18 \pm 3.69 | 6.87 \pm 9.49 | FB |
| Temperate coniferous forests | 11 | 0.94 \pm 0.92 | 4.86 \pm 3.68 | 13.6 | FB |
| Mediterranean forests, woodlands and scrubs* | 9 | 0.33 \pm 0.29 | 1.13 \pm 0.66 | 10.56 | FB |
| Boreal forest / taiga | 4 | 6.42 \pm 5.86 | 13.79 \pm 8.64 | 35.7 | OB |
| Tropical and subtropical grasslands, savannas and shrublands* | 5 | 0.13 \pm 0.12 | 6.06 \pm 2.70 | NA | OB |
| Temperate grasslands, savannas and shrublands* | 14 | 2.43 \pm 3.36 | 4.52 \pm 4.08 | 26.6 \pm 19.7 | OB |
| Montane grasslands and shrublands | 4 | 3.87 \pm 2.89 | 12.49 \pm 7.84 | NA | OB |
| Deserts and xeric shrublands* | 6 | 2.59 \pm 1.31 | 7.66 \pm 8.60 | 52.75 | OB |

* Indicates biomes where studies in agricultural streams ($> 10\%$ agriculture) were found and included in this meta-analysis.

Table 2.3. GPP model summary with complete cases of PAR and ag ($n = 124$) and ER model summary performed with complete cases of GPP, %ag, DIN, SRP, discharge, temperature, light-limitation ($n = 107$).

| Gross primary production | | | | | |
|--------------------------|-------------|------|-----|--------|--------|
| | Coefficient | SE | DF | t | P |
| <i>Intercept</i> | -2.35 | 0.21 | 104 | -11.41 | 0.00 |
| Biome type | -1.13 | 1.16 | 104 | -0.97 | 0.33 |
| PAR | 0.48 | 0.07 | 104 | 6.10 | 0.00 |
| Ag | 1.27 | 0.34 | 104 | 3.73 | 0.0003 |
| Biome type*PAR | 0.73 | 0.33 | 104 | 2.20 | 0.029 |
| Biome type*Ag | -1.60 | 0.47 | 104 | -3.38 | 0.001 |
| Ecosystem respiration | | | | | |
| <i>Intercept</i> | 0.19 | 0.33 | 93 | 0.56 | 0.576 |
| GPP | 0.12 | 0.04 | 93 | 3.17 | 0.002 |
| DIN | 0.08 | 0.04 | 93 | 1.99 | 0.049 |
| Q | 0.18 | 0.05 | 93 | 3.74 | 0.003 |

Table 2.4. Environmental factors in watersheds dominated by agricultural pasture ($n = 78$) and row-crop systems ($n = 33$).

| | Pasture systems | Row-crop systems |
|-----------|--------------------|---------------------|
| P/R | 0.3 ± 0.4 | 0.7 ± 0.4 |
| Ag | 37.4 ± 30.6 | 40.1 ± 40.1 |
| PAR | 19.4 ± 20.1 | 26.3 ± 17.2 |
| canopy | 24.2 ± 25.7 | 24.5 ± 26.2 |
| Drainage* | 547.6 ± 2041.9 | 9.3 ± 12.4 |
| Q | 58.5 ± 62.7 | 30.1 ± 46.1 |
| Width** | 2.8 ± 1.6 | 1.8 ± 0.9 |
| D50* | 87.2 ± 17.1 | 9.6 ± 17.0 |
| Temp | 17.1 ± 2.4 | 17.0 ± 5.2 |
| DIN | 360.5 ± 593.5 | 1008.6 ± 1766.1 |
| SRP | 694.2 ± 4296.7 | 69.3 ± 204.0 |

*Indicate variables with equal variance that significantly differed between agricultural types (Wilcoxon rank-sum test for variables, $p < 0.05$); ** Indicate significant differences for variables with unequal variance ($p < 0.05$, Kolmogorov-Smirnov test). Variable names shown in Table 2.1.

Figures

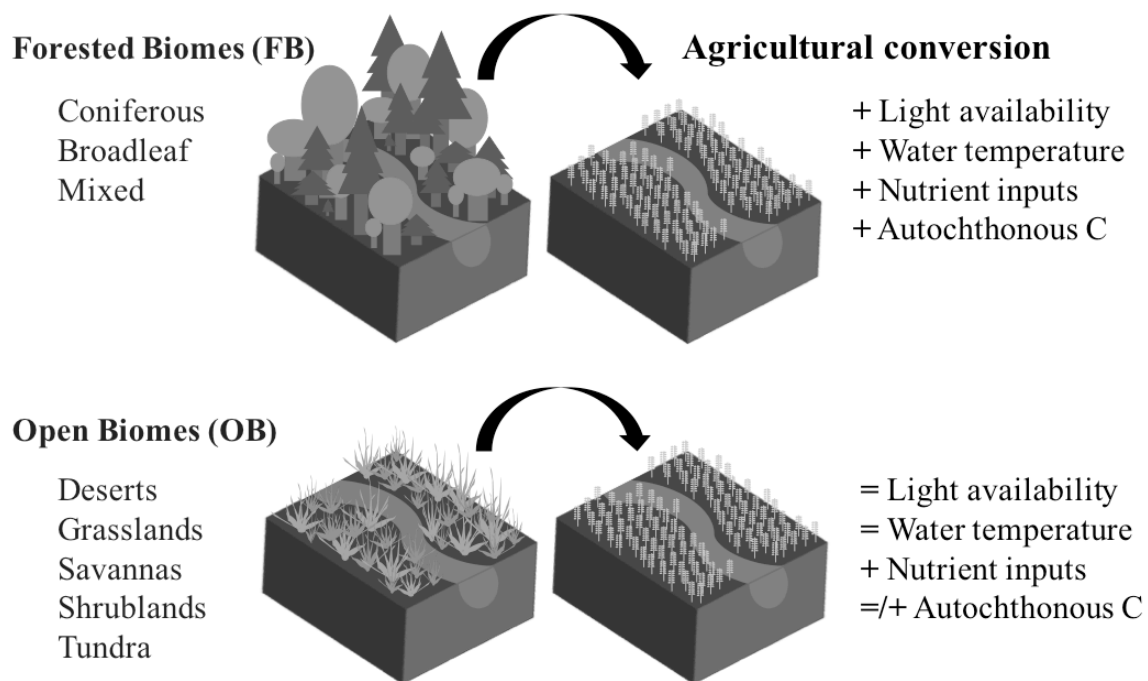


Fig. 2.1. Diagram of the effects of natural ecosystems conversion to agricultural land use in biomes with open riparian vegetation canopies (OB) and biomes with forested riparian vegetation (FB).

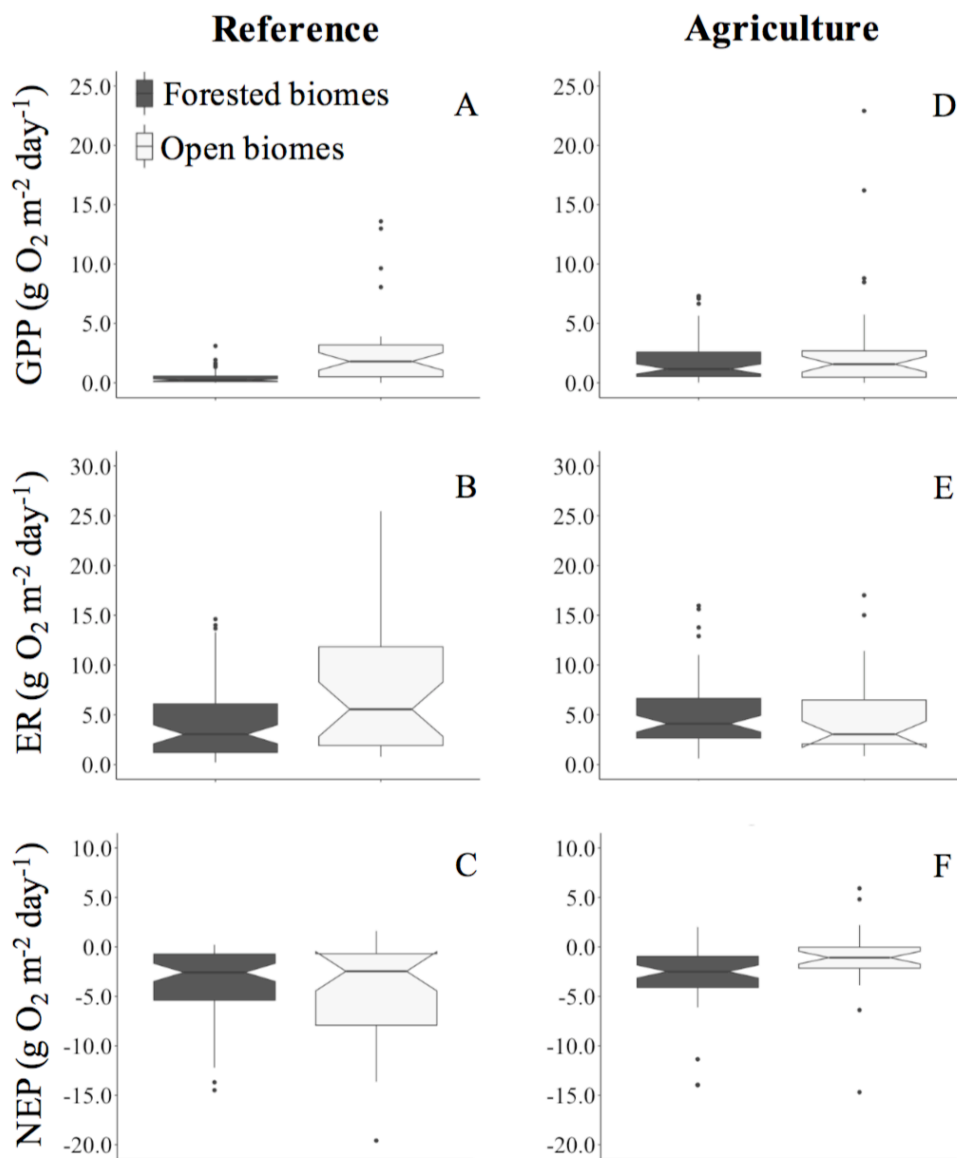


Fig. 2.2. Boxplots of metabolic parameters in reference ($\leq 10\%$ agriculture cover) and agricultural streams ($>10\%$ agriculture cover) in biomes with strong light limitation (FB) and low light limitation (OB). GPP = gross primary production; ER = ecosystem respiration; NEP = Net ecosystem production.

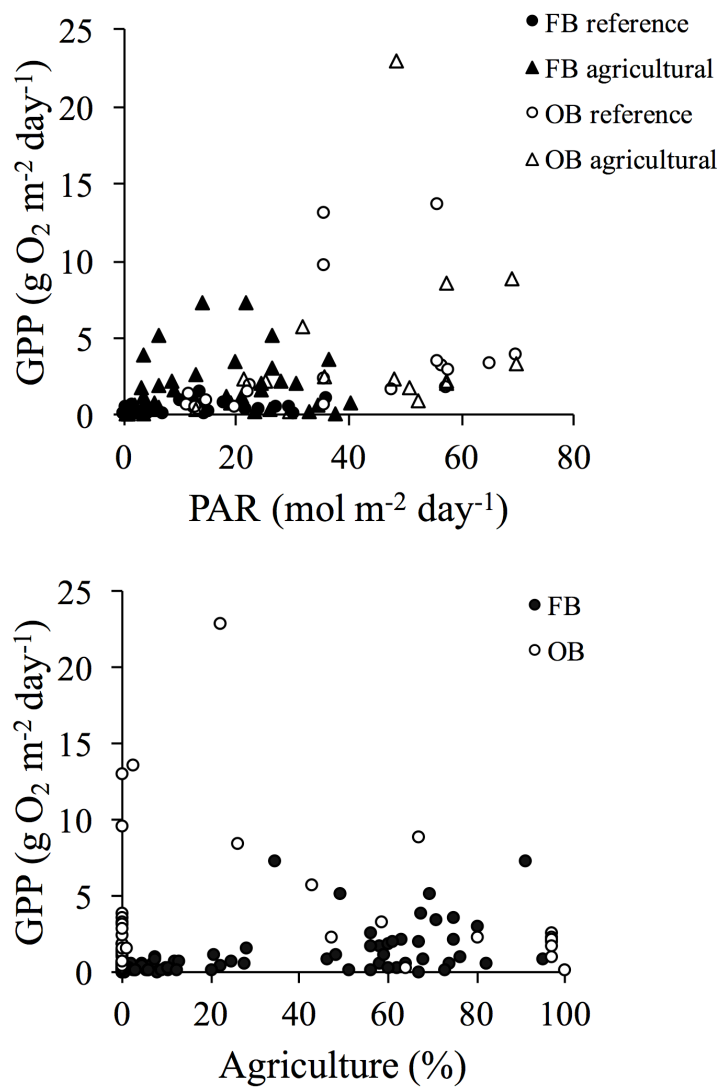


Fig. 2.3. Relationship between gross primary production (GPP) and % agriculture cover (a) and photosynthetically active radiation (PAR) (b) in forested biomes (FB) and open biomes (OB).

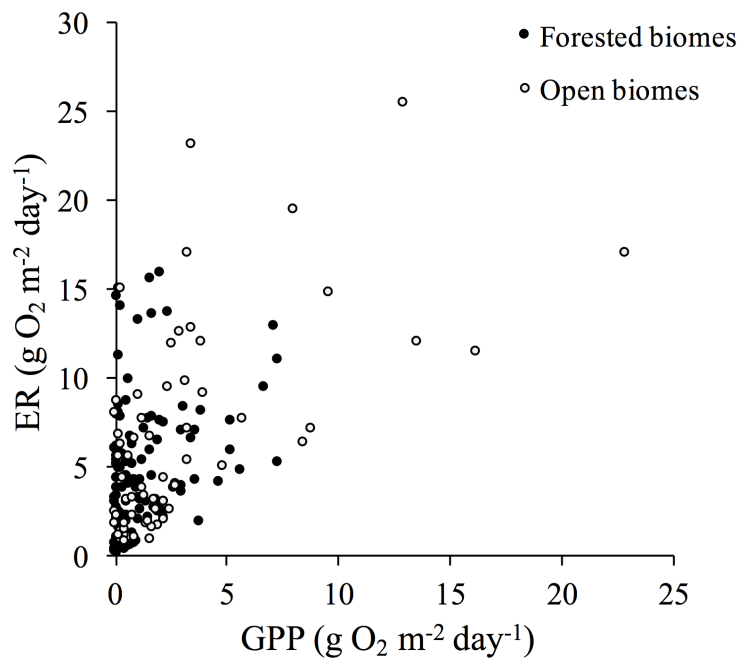


Fig. 2.4. Relationship between gross primary production (GPP) and ecosystem respiration (ER), in forested biomes (FB) and open biomes (OB).

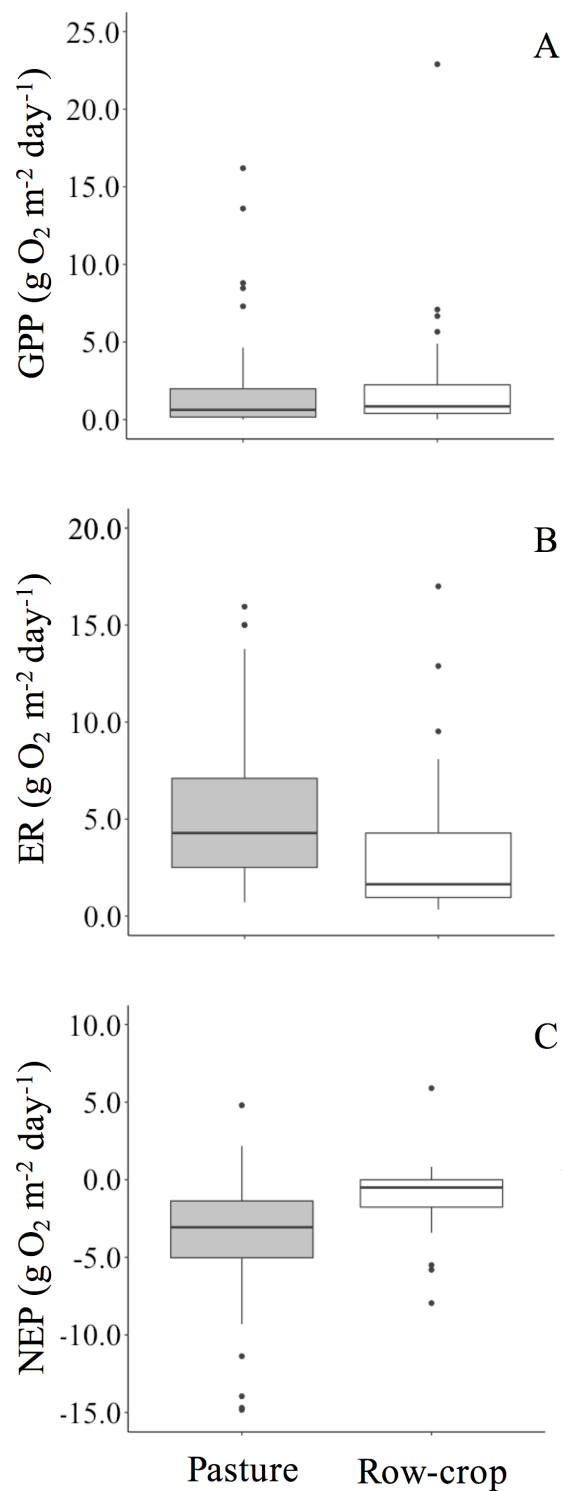


Fig. 2.5. Boxplots of metabolic parameters in streams draining row-crop ($n = 33$) and pasture ($n = 74$) agricultural systems. GPP = gross primary production; ER = ecosystem respiration; NEP = net ecosystem production. Boxes indicate the 1st and 3rd quartiles, lines within each box show the median.

Appendix

Appendix A1 Summary of studies found in literature review and used to build the data base for meta-analysis of agricultural impacts on stream metabolism ($n = 23$ studies; 195 streams).

Table A1.

| Citation | Site | Country | Biome* |
|--------------------------|---|---------------|-------------|
| Acuña et al. 2011 | La Choza, Pampa | Argentina | 8 |
| Alnoee et al. 2015 | 2 streams, Öland | Sweden | 8 |
| Bernot et al. 2010 | 42 streams, Inter-region | United States | 1, 4, 8, 13 |
| Bott and Newbold 2013 | 3 streams, Amazon | Peru | 1 |
| Bott et al. 2006 | 22 stream reaches | United States | 4 |
| Clapcott et al. 2010 | 14 streams 2 streams, New Mexico and | New Zealand | 4, 10 |
| Fellows et al. 2006 | Tennessee | United States | 4, 5 |
| Giling et al. 2013 | 2 streams, Goulburn Broken | Australia | 4, 8 |
| Griffiths et al. 2013 | 6 streams, Northern Indiana | United States | 8 |
| Gücker et al. 2009 | 6 streams, Cerrado | Brazil | 7 |
| Hall and Tank 2003 | 10 streams, Grand Teton | United States | 5 |
| Larson et al. 2016 | 6 streams, Osage prairie | United States | 8 |
| Leggieri et al. 2013 | 3 streams, Pampa | Argentina | 8 |
| Masese et al. 2016 | 9 streams, Mau Escarpment | Kenya | 1 |
| McTammany et al. 2007 | 18 streams, Appalachia | United States | 4 |
| Mulholland et al. 2001 | 3 streams | United States | 4 |
| O'Brien et al. 2014 | 3 stream reaches | New Zealand | 10 |
| Ortega-Pieck et al. 2017 | 9 stream reaches | Costa Rica | 1 |
| Rasmussen et al. 2011 | 4 streams, Hengill 1 stream, north-central | Iceland | 6 |
| Roley et al. 2014 | Indiana | United States | 8 |
| Schäfer et al. 2012 | 7 streams, southern Victoria | Australia | 4 |
| Silva-Junior et al. 2014 | 10 streams, Paraná basin | Brazil | 7 |
| Von Schiller et al. 2008 | 10 streams, Catalonia | Spain | 12 |

* Biomes: (1) Tropical and subtropical moist broadleaf forest; (4) Temperate broadleaf and mixed forests; (5) Temperate coniferous forests; (6) Boreal forest / taiga; (7) Tropical and subtropical grasslands, savannas and shrublands; (8) Temperate grasslands, savannas and shrublands; (10) Montane grasslands and shrublands; (12) Mediterranean forests, woodlands and scrubs; (13) Deserts and xeric shrublands.

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Appendix A2 Distribution of metabolic rates in reference ($\leq 10\%$ agriculture cover) and agricultural streams ($<10\%$ agriculture cover) in biomes with forested riparian vegetation (FB) and open riparian vegetation (OB).

Table A2.

| | Distribution | GPP (g O ₂ m ⁻² day ⁻¹) | ER (g O ₂ m ⁻² day ⁻¹) | NEP (g O ₂ m ⁻² day ⁻¹) |
|---------------------|-----------------|--|---|--|
| Reference FB | Lower one-third | 0.1 | 1.2 | -5.4 |
| This study | Upper one-third | 0.6 | 6.1 | -0.7 |
| | Minimum | 0.004 | 0.2 | -14.5 |
| | Maximum | 3.1 | 14.6 | 0.2 |
| | Reference OB | Lower one-third | 0.51 | 1.9 |
| This study | Upper one-third | 3.2 | 11.8 | -0.7 |
| | Minimum | 0.0 | 0.8 | -19.6 |
| | Maximum | 13.6 | 25.5 | 1.6 |
| | Agricultural FB | Lower one-third | 0.54 | 2.65 |
| This study | Upper one-third | 2.6 | 6.7 | -1.0 |
| | Minimum | 0.02 | 0.06 | -14.0 |
| | Maximum | 7.3 | 16.0 | 2.0 |
| | Agricultural OB | Lower one-third | 0.5 | 2.1 |
| This study | Upper one-third | 2.7 | 6.5 | -0.04 |
| | Minimum | 0.0 | 0.8 | -14.7 |
| | Maximum | 22.9 | 17.0 | 5.8 |
| | Reference | Lower one-third | 0.2 | 3.1 |
| Bernet et al., 2010 | Upper one-third | 1.8 | 9.8 | -1.8 |
| | Minimum | 0.1 | 0.4 | -19.6 |
| | Maximum | 3.9 | 23.1 | 0.0 |
| | Agricultural | Lower one-third | 0.8 | 4.1 |
| Bernet et al., 2010 | Upper one-third | 3.9 | 7.6 | 0.0 |
| | Minimum | 0.1 | 0.9 | -12.6 |
| | Maximum | 16.2 | 15.7 | 4.8 |

Appendix A3 Potential autotrophic C available for consumers in reference and agricultural streams belong to forested biomes (FB) and biomes with open riparian vegetation (OB). All studies used the 90th percentile quantile regression methodology proposed by Hall and Beaulieu (2013) to obtain AR_f .

Table A3.

| Author | AR_f | Autotrophic C available for consumers ($\text{g C m}^{-2} \text{ day}^{-1}$)* | | | |
|--------------------------|--------|---|-------------|-------------|-------------|
| | | Forested biomes | | Open biomes | |
| | | Reference | Agriculture | Reference | Agriculture |
| Hall and Beaulieu, 2013 | 0.44 | 0.08 | 0.33 | 0.48 | 0.57 |
| Hall and Beaulieu, 2013 | 0.63 | 0.05 | 0.22 | 0.32 | 0.37 |
| Griffiths et al., 2013 | 0.72 | 0.04 | 0.17 | 0.24 | 0.28 |
| Roley et al., 2014 | 0.6 | 0.06 | 0.24 | 0.35 | 0.40 |
| Hotchkiss and Hall, 2014 | 0.24 | 0.11 | 0.45 | 0.66 | 0.77 |
| This study | 0.67 | 0.05 | 0.20 | 0.29 | 0.33 |
| Average | 0.56 | 0.06 | 0.26 | 0.38 | 0.45 |

* Stream metabolism measures of O_2 (g O_2) were converted to units of carbon (C) using a photosynthetic quotient (PQ) of 1.2. after Bott (2006), with the equation:

$\text{g C} = \text{g O}_2 \times (1/\text{PQ}) \times (12/32)$; where 12 is the atomic weight of C, and 32 is the molecular weight of O_2 .

Chapter 3: Using remotely sensed imagery of surface water dynamics to estimate fish yield from small reservoirs

Abstract

Globally, inland fisheries are key sources of nutrients for human populations in developing countries. Small reservoir fisheries are particularly important for increasing food security and social resilience in areas with high climatic variability with large populations depending on subsistence agriculture, such as the semi-arid regions of Western Africa. However, small reservoir fisheries resources have not been well integrated into development agendas due to the limited understanding of their magnitude at regional scales. Hence, tools are needed to estimate and gain a quantitative view of fish yields from small reservoirs with limited data availability and monitoring capacity. Here, we studied reservoirs in the semi-arid Volta Basin to develop a codified method to estimate potential fish yields across large areas by pairing remotely sensed surface water dynamics with an empirical model of fish yield. We also compared two different empirical models to estimate fish yields with field data and explored the influences of reservoir sedimentation. Our results show that remotely sensed water dynamics represent a way forward to gaining a better understanding of small reservoir fish production across large semi-arid landscapes. Our approach can be incorporated into models of food provisioning ecosystem services to understand climate impacts, or to support integrated water management to optimize crop, livestock and fish production. Including small reservoir fisheries in the toolset to increase food security may help prioritize governmental and international aid interventions and guide investments in infrastructure.

Introduction

Satisfying the food demands of a growing global population in a rapidly changing world is one of society's biggest challenges (Foley et al., 2011). The spatial and temporal patterns in stored freshwater availability is a key component of food production, particularly in regions of the world with subsistence agriculture-based populations and high rainfall variability (FAO 2009, Rockström et al., 2007). A common solution to improve food security in semi-arid environments is building small reservoirs to store water to support agricultural activities during the dry season. Although geographically widespread, our understanding of the impact

of small reservoirs on food production, particularly fish, is limited due to the lack of fisheries data at regional scales (Welcomme et al., 2011). Yet, data and analytical methods are needed to quantify potential fish yield across large landscapes. Improving the ability to quantify the impact of small reservoirs on food production at is critical for decision making and achieving food security (Molden, 2007; DeFries and Nagendra, 2017).

Some of the most vulnerable human populations globally are located in semi-arid areas of western Africa. These regions are highly threatened by water scarcity, biodiversity loss, desertification, food insecurity, limited access to health services (UNCCD, UNDP, UNEP, 2009; Vörösmarty et al., 2010), and are among the most climatically sensitive zones globally (Vetaas and Kolding, 1991; IPCC, 2013). Since the 1960s, various aid agencies have constructed small dams (capacity < 1Mm³) across the dry region of the western Africa south of the Sahel Desert, referred to as the West Sudanian region (Fig. 3.1). The intended goal of these reservoirs was to store water for livestock and extend crop production (Bajiot et al., 1997; Kolding et al., 2016). An indirect benefit of small reservoirs is the prolonged availability of fisheries resources, which were previously tied to the intermittent nature of semi-arid streams (Bajiot et al., 1997). Small reservoir fisheries in this region are particularly important for human nutrition and for increasing population resilience by diversifying available food sources (IPCC, 2013; Little et al., 2001; Heck, 2007; Kawarazuka and Béné, 2011). Yet, these fisheries resources have been poorly integrated into regional decision-making, mainly due to the complexity of estimating fish production, and difficulty in collecting data given their numbers and widely distributed nature (Dugan et al., 2007; Welcomme, 2011; DeGraaf et al., 2015; Kolding et al., 2016).

To understand the magnitude of fish yields with limited or no data availability, researchers have developed different analytical approaches to relate coarse biological, chemical or morphometric attributes to fish yield (Crul, 1992). Among these, the Morpho-Edaphic Index (MEI) has been widely used to estimate potential fish yield from African lakes and reservoirs (e.g. Henderson and Welcomme, 1974; Marshall, 1984). A major limitation of the MEI is that it does not account for the dynamic nature of semi-arid reservoirs; here, fluctuations in river inputs of water drive aquatic productivity through the episodic delivery of nutrients (Wantzen et al., 2008). In addition, the MEI requires field measures of water chemistry which limits its application at large scales. To incorporate reservoir dynamics Kolding and van Zwieten

(2012) introduced the Relative Lake Level Fluctuation index (RLLF) and showed that the RLLF calculation correlates well with reservoir fish yield. Both indices are designed to estimate yields at coarse scales, not individual water bodies, and use regionally developed empirical correlations developed from reservoirs across parts of Asia and Africa. One key advantage of the RLLF over the MEI is that water level fluctuations can be monitored remotely through empirically derived models of reservoir shape and freely available satellite imagery such as Landsat (Liebe et al 2005; DeGraaf et al., 2015).

Remote sensing reservoir studies in semi-arid western Africa have focused on understanding water availability and dynamics. For example, past studies have used Landsat ET and ETM imagery to estimate the number and volume of small reservoirs (Cecchi et al., 2009; Jones et al., *In prep*; Liebe et al., 2005). Others have used radar imagery from Envisat to assess changes in small reservoir water storage (Liebe et al., 2009) or for delineating small reservoirs (Annor et al. 2009). Kaptué et al. (2013) developed a method to characterize the spatial and temporal variability of surface water in the Soudan-Sahel region using MODIS. While understanding water dynamics is critical for management, none of the aforementioned studies used their findings or focused on providing a methodology to understand fish production. Only one study in lake Turkana, the world's largest desert lake, related water level fluctuations with fish yields using actual catch data and water levels (1993-2014) obtained from the Global Lakes and Reservoirs Database of the USDA (Gownaris et al., 2016). To date, no research has been done to remotely sense small reservoir surface water dynamics to quantify potential fish yields across large semi-arid areas.

The overall goal of this project was to develop a codified method to quantify fish yields in small dry-land reservoirs over large regions using available data. We coupled remotely-sensed data with field data in small reservoirs in the Volta Basin to estimate potential fish yields from hydrological attributes of reservoirs ranging from 1-50 ha in size. Specifically, we (1) compared estimated fish yields via the MEI and the RLLF in two sites using field data, (2) estimated fish yields at five sites during 2000-2016 using satellite-data to understand potential yield variation and fish production over time, (3) compared the influence of storage capacity loss due to sedimentation at two sites. We discuss the implications for international development and the resilience of food production in areas of water scarcity with high climate variability.

Methods

Study area

The study area is located within the 104,749 Km² Nakambé (ex-White Volta) sub-basin of the Volta River Basin, in the semi-arid region of north eastern Ghana at an elevation of range of 180-280 m above mean sea level (Fig. 3.1). Climate patterns are strongly influenced by the migration of the intertropical convergence zone (ITCZ) which drives a unimodal 5-6 month rainy season typically going from May to September (Bajiot et al., 1997). Mean annual rainfall falls between 700-900 mm (Roudier et al., 2014). Due to the ITCZ migration, rainfall patterns exhibit considerable variation across years and climate variability is expected further increase with global climate change (Zeng, 2003; IPCC, 2013). Vegetation is Sudanian Savanna characterized by deciduous *Combretaceae* and *Leguminosae* trees, with shrubs, grasses and herbs in the understory (White, 1983). A large proportion of soils have low vegetation cover due to poor land management practices which has resulted in high erosion rates (Quansah, 2001). These regions are inhabited by subsistence farmers with seasonal open grazing of livestock (Adwubi et al., 2009). Small reservoirs are common across the landscape and represent an essential water resource, particularly during the dry months when surface water is scarce (Cecchi et al., 2009b). In general, small reservoirs are shallow with mean depths ranging from < 1 m to 2.7 m, and have high evaporation rates (Bajiot et al., 1997). At full storage capacities, reservoir areas in our study reservoirs ranged from 3.3 to 39.2 ha (Table 3.1).

Field data collection

We collected field data during April of 2016 in five reservoirs, at the end of the dry season with low reservoir levels. All reservoirs were still holding water. We collected morphological and bathymetric data at all sites and we monitored water electrical conductivity (EC) and water levels at BIN and TANB in nine occasions between April 2016 and January 2017, capturing the minimum and maximum annual water levels. To measure changes in water level we used staff gages. We measured EC with a hand-held device at the edge of the water in three different locations along the dam wall and obtained a single average value (Combo pH/Conductivity/TDS Tester, HANNA instruments, Inc., USA). Since all reservoirs were

shallow and well mixed, we did not expect the measures of EC to differ from other locations or depths in the reservoir.

Reservoir bathymetry

To collect information on reservoir bathymetry in areas with no water, we took high resolution photos from an unmanned aerial vehicle (Phantom III advanced drone with Gimbal camera, DJI, China). We created a digital elevation model (DEM) using the Agisoft software (Fig. 3.2). The cell size of each DEM was < 0.5 m. For the bathymetry measurements in areas still holding water, we measured depth from a boat on a single transect along the long axis of the reservoir. We made depth measurements approximately every five meters and recorded a GPS location. In GIS, we traced the water's edge from our ortho-photographs. We generated bathymetric surface using a spline function in ArcGIS (ESRI, Redlands, California) after assigning a value of zero to water edges and merging the water depth points. We merged the splined bathymetric surface into the DEM to get a single DEM including the entire reservoir area. We then calculated maximum storage capacity by summing the cell depths below the observable spillway height on each reservoir.

Reservoir water dynamics from remotely sensed data sources

First, we compiled monthly composites of Landsat 7 imagery using Google Earth Engine (GEE) and isolated surface water using multiple indices. We tested three normalized difference water indices (Gao, 1996; Xu, 2006):

$$\text{NDWI} = (\text{band 2} - \text{band 4}) / (\text{band 2} + \text{band 4})$$

$$\text{MNDWI5} = (\text{band 2} - \text{band 5}) / (\text{band 2} + \text{band 5})$$

$$\text{MNDWI7} = (\text{band 2} - \text{band 7}) / (\text{band 2} + \text{band 7})$$

Where 2 is the green wavelength, 4 is the near infrared, 5 is the short-wave infrared and 7 is the short-wave infrared. For each index, we tested thresholds to separate water from soil ranging from -1.0 to 1.0 and calculated areas every 0.01 increment. The output of this step was a kml. file with monthly areal data for each parameter set (i.e. water index + threshold). To validate these estimates, we digitized areas using high resolution aerial photos available in Google Earth (GE). Depending on availability, these aerial photographs represent both low and high water conditions, including the reservoir's maximum extent (4-7 per site). To select

the parameter set yielding the best fit between the Landsat and the high resolution aerial imagery, we ran a sensitivity analysis by performing linear regressions between Landsat and the high resolution aerial photos in R Statistical Software (version 3.3.1; R Development Core Team, Vienna, Austria). From the sensitivity analysis, we selected the parameter set with the highest R^2 value and a slope closest to unity (Table 3.2).

Next, in GEE we imported available images of Landsat 5, 7 and 8 imagery dating back to 1984, 1999 and 2013, respectively. We stacked all Landsat images and averaged the pixel values to get a single monthly mean value per pixel. We excluded all images with >25% of cloud cover. We clipped each composite with the digitized polygon representing the maximum areal extent and used the selected parameter set to apply the normalized difference calculation to each clipped monthly composite. We then extracted the area for each polygon and exported the polygon into a GIS database (Fig. 3.2).

To estimate volume for each water surface polygon, we overlaid each water polygon onto the bathymetric surface to determine the elevation of the water's edge. We then subtracted this height from the spillway height, and summed these elevation values under the water surface to obtain an estimate of water volume for each date. Note that this volume is an estimate of water stored using bathymetric surface from 2016, not the date of initial construction. We estimated average water depth by dividing water area by volume.

We used each reservoir's bathymetric map and the remotely-sensed surface water areas to calculate water level fluctuations (i.e. difference between maximum and minimum levels) during 2016. We obtained the maximum depth to area relationship at each site by fitting a line between these two variables during reservoir minimum and maximum areal extents. We used the line equations to obtain a value of maximum depth during the smallest reservoir area for each year (from 2000 to 2016) and we subtracted this value to the depth at full storage capacity.

Estimates of potential fish yields

We used the morpho-edaphic index (MEI) (Ryder, 1956) and the seasonal relative lake level fluctuation index (RLLF) (Kolding and Zwieten, 2012) to compare potential fish yields at BIN and TANB estimated with different indices. We calculated the MEI as:

$$MEI = \frac{EC}{depth}$$

Where EC is the nine-month averaged electric conductivity in $\mu\text{S cm}^{-1}$ and depth is the average depth in meters during the monitored months, estimated from the remote sensing analyses. We estimated the RLLF estimates as:

$$RLLF = \frac{\text{Mean lake level amplitude}}{\text{mean depth}} * 100$$

Where lake level amplitude represents the average seasonal pulse amplitude in meters, obtained by subtracting the annual minimum from the maximum water level, and mean depth is the same as the value described above used to calculate the MEI. Next, to get an estimate of potential fish yields we fitted our MEI and RLLF values to the empirical equation developed for African reservoirs in Marshall (1984) (1) and Kolding and Zwieten (2012) (2):

$$Yield (Kg ha^{-1} y^{-1}) = 23.281 MEI^{0.447} \quad (1)$$

$$Yield (Kg ha^{-1} y^{-1}) = 37.77 RLLF^{0.32} \quad (2)$$

To predict potential annual variations in fish yields, we calculated a RLLF value for every year and fitting to the yield equation. To ensure that we captured the full amplitude of the water levels we only used years which had ≥ 4 monthly satellite images per year (Table A4). Our final data set for this analysis included 2000-2016 data because most previous years since 1984 either had no images or <4 months per year, mainly representing the dry season.

Storage capacity losses and fish yields

To estimate reservoir storage capacity losses due to sedimentation and its potential influence on fish yields, we obtained initial reservoir storage capacities at the time of dam construction for two of the five study reservoirs (BID and SUM, DGRE, 2016, Lacrosep Phase I- GIDA, 2017). At these two sites, we compared the maximum stored volume from our DEM to the maximum volume at construction to calculate losses in stored volume. We then divided the lost volume by the age of dam to get an annual value of storage capacity loss. To calculate annual depth decreases due to sedimentation, we calculated the initial and the current reservoir depths by dividing the volume at the time of construction and the present volume by the maximum area, respectively. We then obtained a measure of total depth loss by

subtracting the current reservoir depth to the construction depth and divided this value by the dam's age to get an annual value. We note that our estimates of infilling rates assumed that infilling occurred at a constant rate and may not accurately represent each year as sediment input are driven by climate.

To understand how sedimentation may have influenced potential yields over time, for each site we computed the RLLF from 2000-2016 from the remotely-sensed water fluctuations using three different depth values. Specifically, we estimated 1) RLLF based on the average depth measured in 2016, 2) RLLF accounting for annual gradual decreases in depth, and 3) RLLF using the estimated average depth at the time of construction to simulate the RLLF without sediment inputs. We then calculated the RLLF for these three scenarios to show change in fish yield over time.

Results

Reservoir water dynamics

Average monthly values of reservoir area for all available years since 1984 (Table A4) showed that reservoirs are smallest around April and May, and peak in size during August or September (Fig. 3.3), coinciding with the regional rainfall patterns. Maximum reservoir areas across all years were ≤ 10 ha in four study sites and reached up to 39.2 ha in BIN. The smallest reservoir was SUM, with a maximum area of < 2 ha. From the dry to the rainy season all reservoir areas significantly increased, with relative increases ranging from 116% in TANS up to 221% in BOY. Mean storage capacities varied widely between study sites going from 1.47 ha-m in the smallest reservoir to 65.1 ha-m in BIN (Table 3.3). In most cases stored volumes decreased with reservoir size except for TANB which was shallow and therefore had lower or similar storage capacities than other smaller reservoirs.

As expected for reservoirs in this region, all reservoirs were shallow, with mean annual depths across sites ranging from 0.6 m to 2.7 m. Throughout the year mean monthly depths were higher during the dry season and decreased as more water filled the reservoir covering shallower areas (Fig. 3.3). Annual water level fluctuations were lowest in BIN and highest in TANS, with values of 35.8 and 148.9. All can be considered highly dynamic systems, particularly SUM and TANS where the average amplitude of water levels exceeded the mean depth (Table 3.3) (Kolding et al., 2016).

Potential fish yields: MEI versus RLLF

We found that potential fish yields in 2016 were 17% higher in BIN and 4% higher in TANB when estimated with the RLLF than with the MEI (Table 3.4). Specifically, potential MEI and RLLF yields were 139.2 Kg ha⁻¹ y⁻¹ and 162.5 Kg ha⁻¹ y⁻¹ in BIN, and 232.2 Kg ha⁻¹ y⁻¹ and 242.4 Kg ha⁻¹ y⁻¹ in TANB. When yields were normalized by reservoir area total yields in BIN were close to half a ton higher when estimated with the RLLF than with the MEI (Table 3.4). In both reservoirs, the 2016 RLLF-yields were above the yields derived from the satellite imagery because the amplitude of water levels was larger when measured in the field than with the remote sensing analysis.

RLLF and potential yield variation over time

Estimates of annual yields based on annual RLLFs derived from the 2000-2016 continuous satellite imagery data set (Table A4) showed that all study reservoirs may be highly productive, with potential median annual yields ranging between 118 and 188 Kg ha⁻¹ y⁻¹ across sites (Fig. 3.4a). The largest variation in potential yields was found in SUM and the reservoir with the lowest variation was TANS. After normalizing yields by reservoir area, we found that median fish yields in BIN were at least twice as high compared to the other four smaller reservoirs. The two smallest reservoirs BOY and SUM had low total fish yields (<1 ton y⁻¹) (Fig. 3.4b).

Potential fish yields accounting for sediment inputs

Storage capacity losses since dam construction up to 2016 were 29% in BIN in 54 years and 70% in SUM in 55 years. Annual decreases in depth were 0.016 m y⁻¹ at BIN and 0.04 m y⁻¹ at SUM, which over the years may have led to a total decrease of 0.88 m and 2.14 m respectively. Given that sediment inputs decrease reservoir depth and depth is in the denominator of the RLLF equation, RLLFs increased with sediment loading. Accordingly, higher RLLF lead to higher potential fish yields per unit of reservoir area. For example, we found that from 2000-2016 BIN may have increased its yields from 108.8 Kg ha⁻¹ y⁻¹ in a scenario with the reservoir not receiving any sediment inputs, to 117 Kg ha⁻¹ y⁻¹ with gradual sedimentation (Fig. 3.5a). The difference between the yields in these two scenarios was larger

in SUM due to higher storage capacities losses in a shorter period of time (2004-2016) (Fig. 3.5b). Basing fish yield estimates on depth values obtained in 2016 and not accounting for changes in depth over time, resulted in the highest yields.

Discussion

We present a method for quantifying fish yields in small reservoirs using available remotely sensed data of temporal surface water dynamics and empirical equations of fish yields. This approach can improve our ability to quantify the value of international investments in small reservoirs in developing countries and trade-offs between land use practices and food production. Ultimately our method can be scaled up to aid decision making aiming at meeting development goals such as improving food security, and to prioritize governmental and international aid interventions.

Static versus dynamic indices

The differences in fish yields estimated via the MEI and the RLLF during 2016 show that the index of choice influences the magnitude of predicted yields. This matter is particularly relevant in reservoirs with larger extents (e.g. BIN versus TANB in this study), where differences between the two indices lead to significant differences in estimated total production, or if this approach is used at larger spatial scales, such as the Volta Basin. When faced with a lack of field validation data, using the index that best reflects the factors driving ecosystem dynamic represents a better approach than using static indices (Laë et al., 1999; Kolding and van Zwieten, 2012). Hence, we reason that in our study region using RLLF to derive fish yields may be more adequate than the MEI because reservoirs are dynamic and water fluctuations likely drive ecosystem productivity (Downing, 1999; Laë, 1997; Wantzen et al., 2008). Furthermore, a critical advantage of using the RLLF versus the MEI to understand fish yields is that the RLLF can be measured using only remote sensing tools allowing predictions across large landscapes and longer temporal scales.

Model performance

Fish yields derived from the 2000-2016 remotely sensed RLLF indicate that fisheries are likely highly productive compared to large reservoirs and fall within the range of small

reservoir yields reported in the literature. To our knowledge, there is only one field measurement of fish yields in a reservoir of similar size in our study region, which found a yield of 170 Kg ha⁻¹ y⁻¹ (Bajiot, 1997). The other field assessments in the region were made in 1968 and found that yields ranged from 35 Kg ha⁻¹ y⁻¹ to 100 Kg ha⁻¹ y⁻¹ (CTFT, 1968). However, these reservoirs were three to ten times larger than our study reservoirs. Thus, the higher yields found in our study could be explained by our reservoirs being smaller than those in the CTFT study because fish productivity is negatively related to reservoirs size (Kolding et al., 2016). Further, the estimated average of 155 Kg ha⁻¹ y⁻¹ across our study sites is also similar to yields found in small reservoirs in southern regions of Africa (Marshall and Maes 1994). Hence, our estimates of fish yields via the RLLF are likely adequate to understand fish availability in the absence of field monitoring capacity. We note that developing empirical equations for our study region would be an ideal scenario (Crul, 1992; Béné, 2007).

One limitation of our approach is that it does not account for reservoir sedimentation and our results show that reservoir storage capacities losses may increase fish yields. The bias in yield estimates depends on the timing and magnitude of storage capacity losses (e.g. SUM versus BIN in this study), and particularly in how mean reservoir depth decreases over time. Thus, the optimal strategy to predict fish yields may be to make a series of yield predictions based on several water depth scenarios derived from known storage capacity losses. Our results and previous studies in our study region, have estimated that annual storage capacity losses range from 0.4% to 3.63% (Adwubi et al., 2009; Shmengler and Vlek, 2015). These numbers could be used to obtain a range of potential yields instead of a single estimate. Further, although our results indicate that fish yields per unit of reservoir area may increase in shallower silted reservoirs, evaporation rates also increase due to higher water temperatures further aggravating water losses and increasing the likelihood of losing fish due to seasonal desiccation (Bajiot, 1997; Kolding et al., 2016).

Implications for development

Estimating fish yields via remote sensing can directly benefit our understanding of the role of small reservoir fisheries in human nutrition in data-poor regions. This is particularly important because small reservoir fisheries in semi-arid regions of Africa are highly resilient to changes in climate, are underexploited and significantly contribute to healthy diets and food security

(Béné, 2007; Kawarazuka, 2010; Béné et al., 2016; Kolding et al., 2016b). Specifically, fish are important sources of protein and small fish in particular can be rich in essential micronutrients and minerals such as vitamin A, zinc and calcium (Heck et al., 2007; Kawarazuka and Béné, 2011). These nutrients are critical across different stages of human development and are generally low in vegetable products (Kawarazuka, 2010). By providing a quantitative view of reservoir fish yields, our approach offers a way to understand fish supply and their potential relative contribution to human diets (Kolding et al., 2016). This information in turn can be used to guide strategies aiming at improving human nutrition and food security (Dugan et al., 2010).

Using empirical equations of reservoir morphology our methodology can be scaled up to a larger number of reservoirs. This information could in turn be incorporated into models of ecosystem services quantifying food provisioning services to assess trade-offs in water allocation decisions or land management practices. Modeling efforts may be used to respond to a variety of questions relating to crops, fisheries, stored water volume, land use and climate. For example, models could be used to define which water allocation decisions lead to higher nutrient production and help prioritize water use for crops or fish based on the amount of available water. Models could also look at the efficacy of riparian buffers and soil conservation practices to reduce sediment inputs to reservoirs, or forecast the effects of droughts on food availability to plan aid interventions. Such an ecosystem service approach could improve population resilience (Dugan et al., 2010) and will likely become more important as climate unpredictability and drought severity increase with climate change (Jul-Larsen et al., 2003; Brander, 2007). Overall, the knowledge derived from food production modeling efforts can support more integral decision-making by viewing reservoir-agriculture as interdependent systems and, optimize their benefits to human populations.

In conclusion, small reservoir fisheries are productive and nutritious food sources that could be better integrated into strategies to improve population nutrition and food security in semi-arid regions of Western Africa. By providing a method to quantify fish yields over large landscapes via remotely-sensed surface water dynamics, this study presents an approach to bridge the gap between the lack of fisheries data and the strategies to improve food security. The information resulting from our methodology can be used to model food provision ecosystem

services in crop-reservoir systems to improve local decision making, increase population resilience and plan international aid interventions addressing food security.

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Tables

Table 3.1. Study reservoir attributes

| Name | Abbreviation | Location | Construction year | Initial storage capacity (m ³) | Max area (ha) |
|----------|--------------|----------------------------|-------------------|--|---------------|
| Binaba | BIN | 10.780195 N -0.47771 W | 1962 | 1'170,000 | 39.2 |
| Boya | BOY | 10.830492 N -0.440651 W | - | - | 9.9 |
| Sumbrugu | SUM | 10.830469 N -0.937905 W | 1961 | 100,000 | 3.3 |
| Tanga B | TANB | 10.916342 N -0.433539 W | - | - | 10.5 |
| Tanga S | TANS | 10.910949 N -0.447629 W | - | - | 10.2 |

Table 3.2. Best parameter set predicting areal extents at each reservoir, showing the fit between the manually-digitized reservoir areas in Google Earth (GE) and the estimated areas in Google Earth Engine (GEE).

| Site | Pairs | Bands | Threshold | Slope | R ² | Y-intercept (Max. area) | P-value |
|------|-------|-------|-----------|-------|----------------|-------------------------|---------|
| BIN | 5 | 2,5 | -0.35 | 0.899 | 0.97 | -3.3 (39.2) | 0.003 |
| BOY | 5 | 2,5 | -0.05 | 1.123 | 0.99 | 1.6 (9.9) | 0.000 |
| SUM | 3 | 2,4 | -0.10 | 1.389 | 1.00 | 0.6 (3.3) | 0.003 |
| TANB | 2 | 2,5 | -0.12 | 1.163 | 1.00 | -1.4 (10.5) | - |
| TANS | 3 | 2,5 | -0.29 | 1.120 | 1.00 | -3.3 (10.2) | 0.013 |

Table 3.3. Reservoir characteristics derived from the remote sensing analysis showing average values (\pm SD) since 1984 or since dam construction.

| Reservoir | BIN | BOY | SUM | TANB | TANS |
|----------------|----------------|----------------|----------------|----------------|-----------------|
| Mean area (ha) | 25.2 \pm 5.0 | 4.52 \pm 1.1 | 1.42 \pm 0.3 | 8.5 \pm 1.0 | 7.3 \pm 1.1 |
| Mean depth (m) | 2.7 \pm 0.3 | 1 \pm 0.12 | 1.1 \pm 0.06 | 0.6 \pm 0.1 | 1.8 \pm 0.2 |
| Volume (ha m) | 65.1 \pm 9.1 | 4.05 \pm 0.7 | 1.47 \pm 0.3 | 4.81 \pm 0.4 | 12.32 \pm 1.3 |
| RLLF-s | 35.8 | 89.1 | 114.6 | 69 | 148.9 |

Table 3.4. Comparison of potential fish yields in 2016 using the morph-edaphic index (MEI) and the relative lake level fluctuation index (RLLF).

| | BIN | TANB |
|--|-------|-------|
| MEI | 43.4 | 125 |
| RLLF | 95.5 | 333.3 |
| Amplitude of water level (m) | 2.55 | 2.1 |
| Yield MEI (Kg ha ⁻¹ y ⁻¹) * | 139.2 | 232.2 |
| Yield RLLF (Kg ha ⁻¹ y ⁻¹) ** | 162.5 | 242.4 |
| Relative yield difference between | | |
| MEI and RLLF (%) | 17 | 4 |
| Ton y ⁻¹ MEI | 2.77 | 1.52 |
| Ton y ⁻¹ RLLF | 3.23 | 1.58 |

*Fitted with equation for African reservoirs in Marshall, 1984.

**Fitted with equation for African reservoirs in Kolding and Zwieten, 2012

Figures

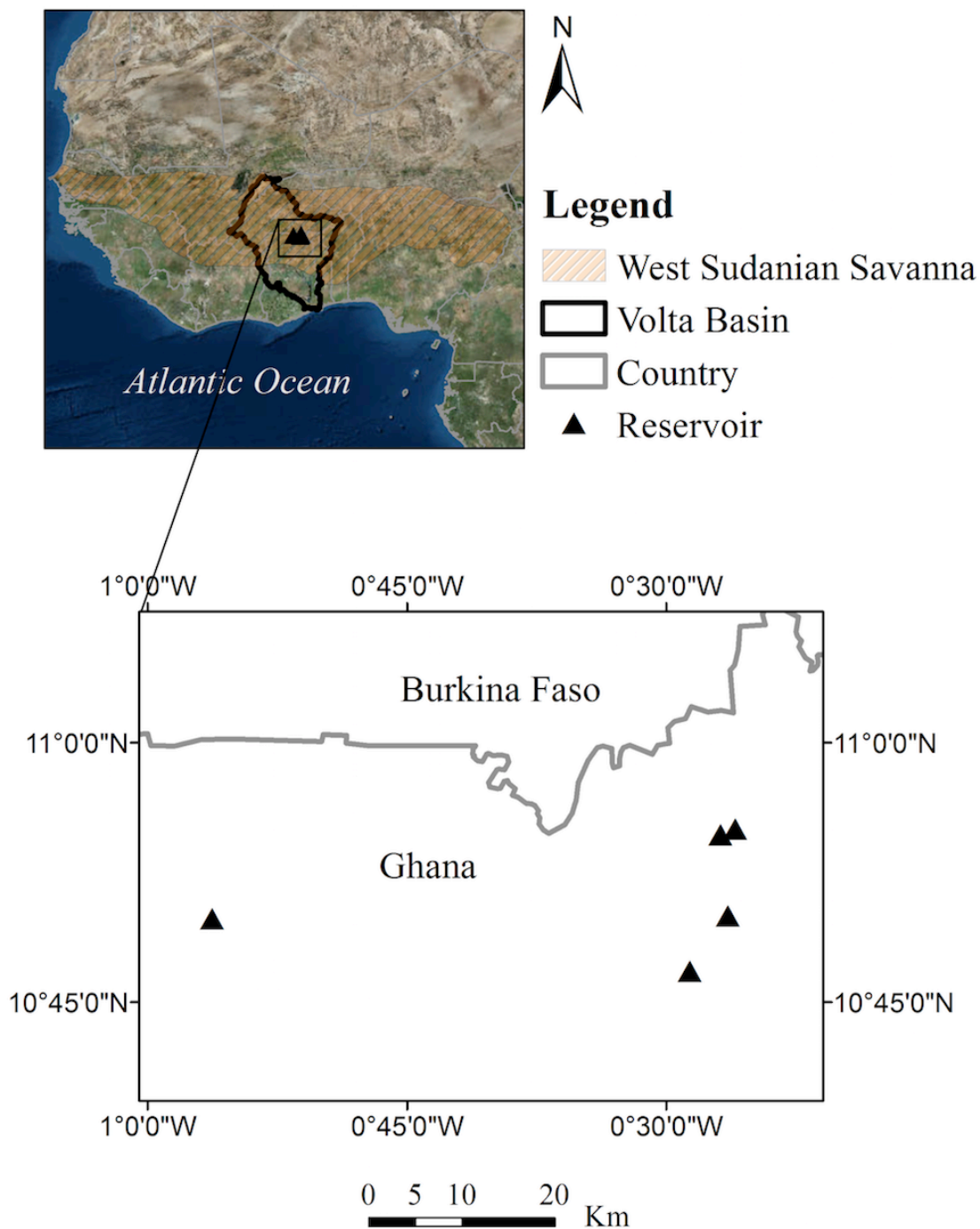


Fig. 3.1. Study area showing the location of the five study reservoirs within the Volta Basin in north eastern Ghana.

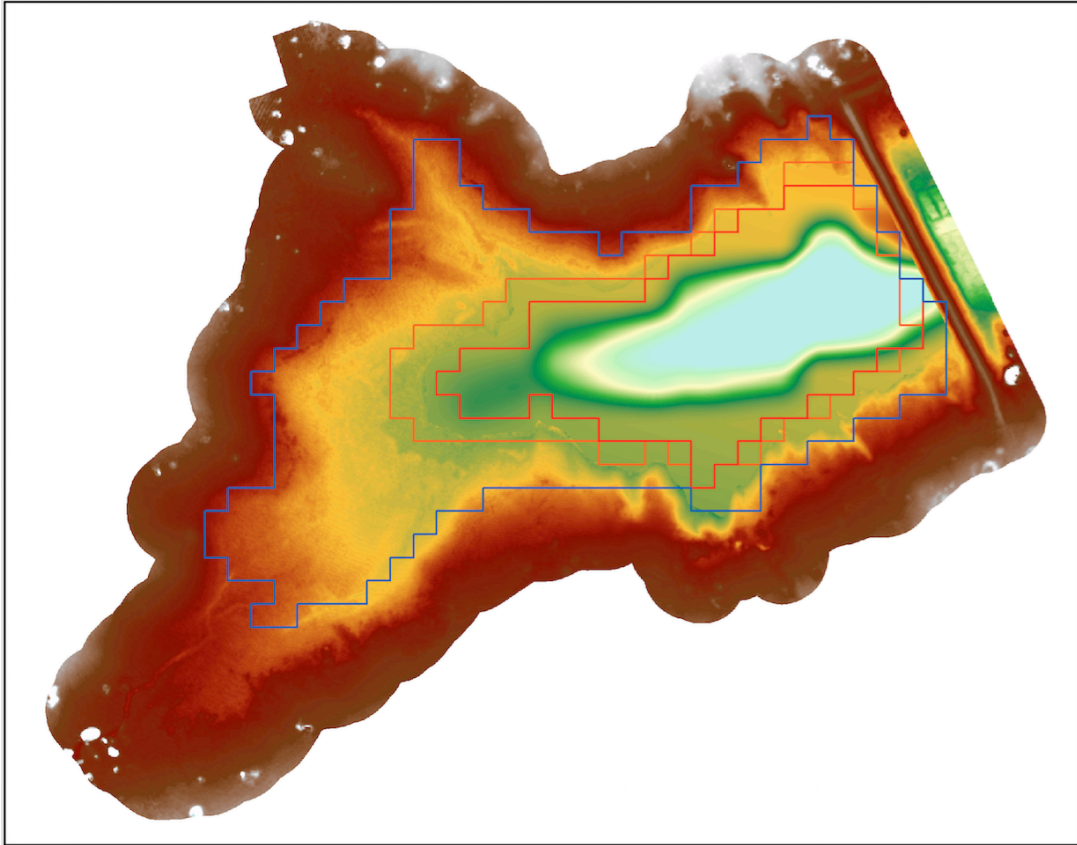


Fig. 3.2. Example of bathymetric map estimated from the unmanned aerial vehicle aerial imagery at Binaba reservoir. The three polygons show different water surface areal extents during 2016 estimated from the Landsat imagery. The two smaller polygons and the large polygon show water levels in April, May and August, respectively.

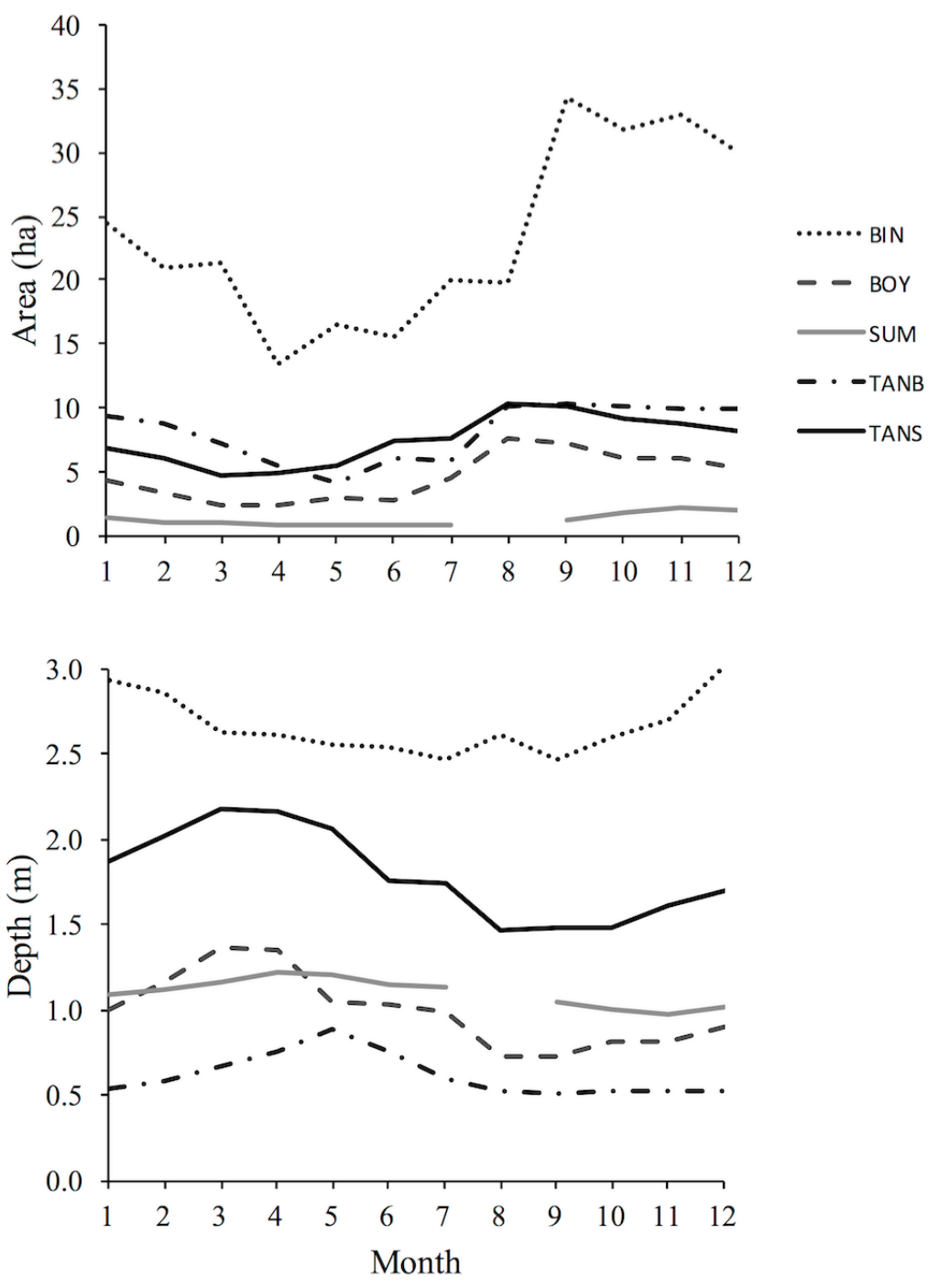


Fig. 3.3. Monthly average depth (m) and reservoir area (ha) since 1984 derived from remote sensing data in five small reservoirs in a semi-arid region. No images were found for SUM during the month of August. The number of images per month at each site ranged from 2 to 20.

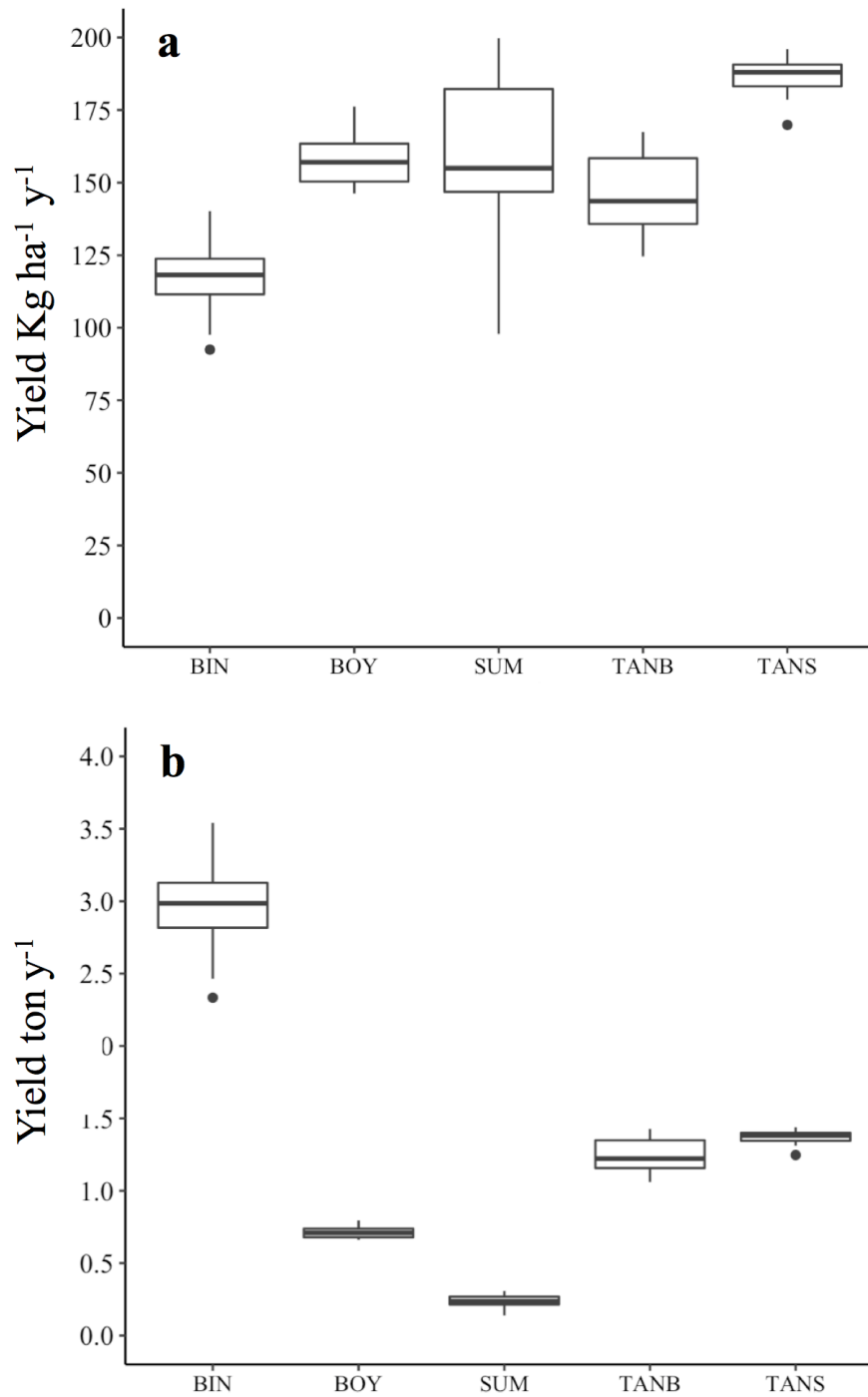


Fig. 3.4. Potential fish yields based on annual estimates of RLLF across five study reservoirs showing a) potential yields per unit of reservoir area, and b) potential fish yields normalized by reservoir area. BIN ($n = 20$); BOY ($n = 21$); SUM ($n = 15$); TANB ($n = 17$); TANS ($n = 21$).

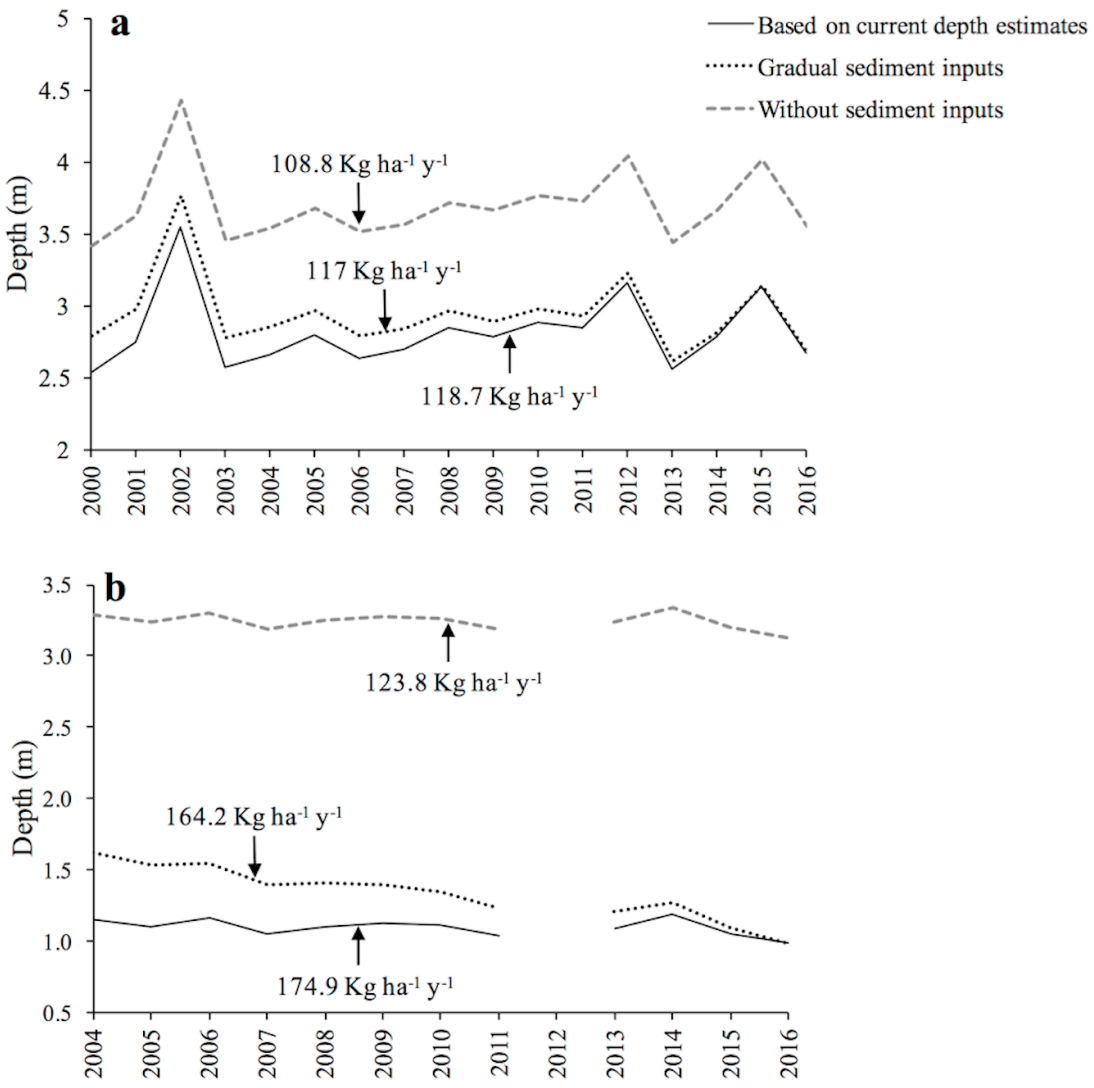


Fig. 3.5. Different scenarios reservoir depths in two sites showing 1) Estimated water levels based on the average depth in 2016, 2) Estimated gradual sediment inputs, and 3) A hypothetical scenario where reservoirs would not receive sediment inputs over time. a) Binaba (BIN); b) Sumbrungu (SUM).

Appendix

Appendix A4 Summary of satellite imagery data sets from 1984 to 2016. Parentheses indicate the proportion of total possible data (i.e. 32 years and 384 months) captures with our remote sensing analysis.

Table A4.

| | BIN | BOY | SUM | TANB | TANS |
|--|----------|----------|----------|----------|----------|
| Total years with at least one satellite image | 30 (94) | 30 (94) | 28 (88) | 21 (75) | 30 (94) |
| Total months covered | 150 (39) | 161 (42) | 111 (29) | 135 (40) | 163 (42) |
| Continuous years with >4 monthly composites to estimate RLLF-s | 17 (53) | 17 (53) | 13 (41) | 17 (61) | 17 (53) |

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