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Autochthonous production in shallow littoral zones of five floodplain rivers: effects of flow, turbidity and nutrients

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SUMMARY

1. Comparative research and generalisations in lotic ecology are challenged by the dynamic hydrology of fluvial systems. The aim of this study was to understand more fully how factors such as light, nutrients and flow can predict variation in autochthonous production and algal biomass.
2. We measured seasonal changes in percent bankfull discharge, inorganic nutrient concentrations, turbidity, instream primary production, respiration and algal biomass in the littoral zone of five floodplain rivers in one temperate and two tropical regions of the Western Hemisphere. The Brazos, Guadalupe and Neches rivers are in Texas, while the Tambopata River is in Peru and the Cinaruco River in Venezuela. Our study rivers represented a range of hydrological regimes, turbidity levels and nutrient concentrations.
3. Flooding patterns were more seasonal in the tropical rivers than in the (temperate) Texas rivers. Inorganic nutrient concentrations were higher in the temperate rivers, probably due to anthropogenic nutrient loading. Turbidity was higher following periods of high flow in the Brazos, Tambopata and Guadalupe rivers than in the Neches and Cinaruco rivers. Littoral zones in the sediment-laden Brazos and Tambopata rivers became heterotrophic during periods of high discharge, while littoral zones in the Guadalupe, Neches and Cinaruco rivers were consistently autotrophic. Regression tree analysis suggested that algal production and biomass in the water column responded more strongly to seasonal changes in nutrients and temperature than to turbidity, while benthic algae responded more strongly to turbidity.
4. Our findings suggest that during periods of high flow and turbidity in rivers containing fine sediments, autochthonous production is limited and terrestrial-based organic matter may assume greater importance in the aquatic food web.

Keywords: hydrology, nutrients, productivity, river, turbidity

Introduction

Biochemical transformations, including photosynthesis and respiration, in rivers take place in the water column and sediments, both of which are influenced by hydrology. Most river ecosystems are net heterotrophic (gross primary production < ecosystem respiration) because of high rates of microbial processing of terrestrial organic carbon (Battin *et al.*, 2008). Regardless, autochthonous production (i.e. instream primary production) often accounts for a large fraction of the organic matter assimilated by metazoans in fluvial ecosystems, probably due to its relatively high nutritional quality (Thorp & Delong, 2002; Roach, 2013). River landscapes are highly heterogeneous and dynamic. Shallow slackwater areas may be important because they retain nutrients that facilitate benthic algal production, which may then be incorporated higher in the food web (Thorp & Delong, 1994; Hein *et al.*, 2005). However, very little is known about how algal primary production in these habitats changes over time in rivers with different physicochemical characteristics and hydrological regimes.

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A recent literature review concluded that catchment characteristics, including flow dynamics and suspended sediment load, strongly influence algal primary production and the structure of river food webs (Roach, 2013). For example, in catchments with highly erodible soils, during periods of high or increasing river discharge, suspension of inorganic sediment can substantially reduce algal primary production through shear stress, abrasion and light limitation (Kirk, 1985; Meade, 1988). In rivers dominated by clay, silt and other fine sediments, aquatic invertebrates and fish have been shown to incorporate a large fraction of terrestrial-based organic matter into tissues, probably because of limitation of autochthonous production during high-flow periods (e.g. Zeug & Winemiller, 2008). During periods of receding or low discharge, water velocity decreases and deposition of inorganic sediment lowers turbidity, resulting in increased primary productivity in shallow habitats (Kirk, 1985; Meade, 1988). Consequently, invertebrates and fish inhabiting rivers that are normally turbid often assimilate large fractions of material from algae following extended periods of low flow (Bunn, Davies & Winning, 2003; Pease *et al.*, 2006; Turner & Edwards, 2012).

We conducted field research to investigate primary production in the shallow, littoral areas of rivers in temperate and tropical regions with diverse catchment and sediment characteristics. We measured seasonal changes in percent bankfull discharge, nutrient concentrations and turbidity, and net ecosystem production (NEP) and algal biomass (chlorophyll *a*) in both the water column and benthos within the littoral zone of five floodplain rivers. Our five study rivers represented a range of hydrological regimes, turbidity and nutrient concentrations, and we anticipated that the high variation in their physicochemical and hydrological characteristics would allow us to tease apart the dominant factors causing variation in algal primary production and biomass in littoral zones. We expected that interactions between flow, nutrients and turbidity would influence autochthonous production in the littoral zone of sediment-laden rivers with high concentrations of inorganic nutrients. In these rivers at high discharge, we expected littoral zones to be heterotrophic and algal biomass to be negligible. At low discharge, we expected littoral zones to be autotrophic and algal biomass to be high. In sediment-laden rivers with low concentrations of inorganic nutrients, we anticipated relatively little algal production regardless of flow. In rivers with less erodible soils, we expected the littoral zone to be autotrophic at both low and high flow, following previous work indicating that the littoral zone is consistently autotrophic when transparency is high (Lewis, 1988; Cotner *et al.*, 2006; Montoya *et al.*, 2006).

Methods

Study sites

This study examined rivers from five catchments with divergent characteristics (listed from most sediment-laden to least sediment-laden): the Brazos River in Texas (30°37′N, 96°30′W), the Tambopata River in Peru (12°47′S, 69°17′W), the Guadalupe River in Texas (28°49′N, 97°01′W), the Neches River in Texas (30°22′N, 94°06′W) and the Cinaruco River in Venezuela (6°32′N, 67°24′W: Fig. 1: Table 1). The Brazos is a lowland river flowing from Blackwater Draw, New Mexico, to the Gulf of Mexico. Although high flows are not predictable seasonally (Zeug & Winemiller, 2008), median flow tends to be higher in winter and spring. Large-scale flooding has been reduced due to flow regulation in upstream reaches, but high flows periodically inundate floodplains of the lower reaches. Mean annual sediment yield of the Brazos River is higher than that of any other river in Texas (Curtis, Culbertson & Chase, 1973). The Tambopata River originates in the Andean piedmont and flows unregulated to the lowland Madre de Dios River in Peru, eventually joining the Amazon River in Brazil. The hydrological regime is seasonal but water-level fluctuations of several metres per day are frequent (Hamilton *et al.*, 2007). The Tambopata River carries high loads of suspended sediments as a result of erosion of the Andes Mountains (McClain & Naiman, 2008). Among the five rivers, the Guadalupe River is under the greatest regulation, with 10 mainstem impoundments in its upper reaches. The Guadalupe River flows from Kerr County, Texas, to the Gulf of Mexico. Much of the base flow in the lower Guadalupe River is provided by springs located in headwaters (e.g. Comal and San Marcos springs). Flow in the lower, floodplain reaches is partially regulated by the U.S. Army Corps of Engineers at the Canyon Lake dam, although overbanking flows are frequent in the lower reaches in spring. The Neches River originates in eastern Van Zandt County, Texas, and flows through the coastal plains to Sabine Lake, a shallow bay connected by a narrow outlet to the Gulf of Mexico. Although the hydrological regime is partially regulated by dams in the upper basin, high flows, generally in spring, can flood riparian wetlands along the lower reaches. The Neches River is 'tea stained' as a result of dissolved organic matter (DOM, humic

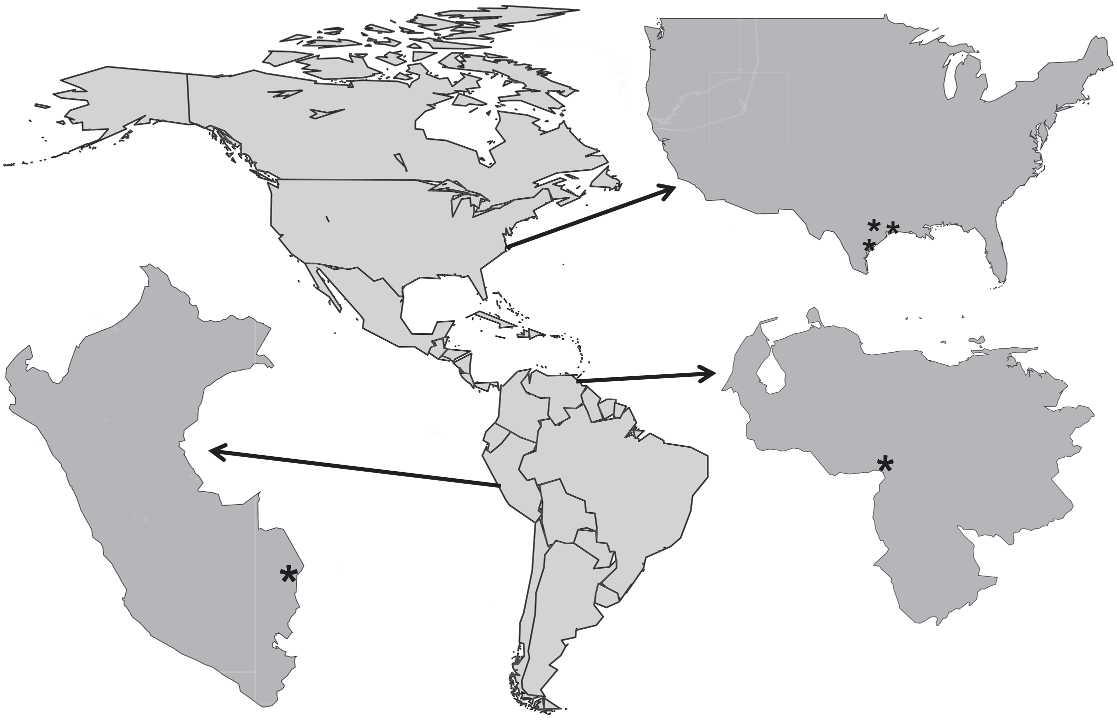

Fig. 1 Map of study sites. The Guadalupe, Brazos and Neches rivers are in the USA (listed from west to east). The Tambopata River is in Peru, and the Cinaruco River in Venezuela.

Table 1 Key characteristics of study rivers (in order of descending sediment load). Measurements were determined for the length of river that was studied. Discharge measurements are not available (NA) for the Tambopata and Cinaruco rivers

Study river	Altitude (masl)	Mean annual discharge (m^3 s^{-1})	Bankfull discharge (m^3 s^{-1})	Mean channel width (km)	Dominant land use in catchment
Brazos	58	138	2076	0.10	Agriculture, cattle production
Tambopata	184	NA	NA	0.20	Small-scale cattle production
Guadalupe	12	55	238	0.05	Agriculture, cattle production
Neches	5	163	869	0.08	Agriculture, cattle production
Cinaruco	45	NA	NA	0.15	Little human use

substances) leached from surrounding wetlands and riparian forests. The Cinaruco River, located in the Venezuelan llanos, is an unregulated tributary of the Orinoco River. The hydrological regime is strongly seasonal with a prolonged annual flood pulse (Montoya *et al.*, 2006). The Cinaruco River is a moderate blackwater river with a high concentration of DOM and low pH. Previous studies measuring sources of DOM and net ecosystem production within the water column of the Cinaruco River have inferred that total DOM is maximised during the annual low-water period when net ecosystem production is highest, suggesting that DOM has little influence on light availability for algae (Cotner *et al.*, 2006; Roelke *et al.*, 2006).

Physicochemical estimates and algal primary production

Percent bankfull discharge, nutrient concentrations (mg L^{-1}) including soluble reactive phosphorus (SRP), NH_4, NO_2, NO_3 and silica (SiO_3 in the Cinaruco River, SiO_2 in all other rivers), turbidity (FTU) and water-column and benthic respiration, algal net ecosystem production and chlorophyll *a* concentration were measured at point sandbars located along the low-velocity side of river meanders. In each river, we made measurements on 3–5 sandbars during different seasons and flow conditions (see Appendices S1 and S2). Each of the variables was measured on the same day, except for the Cinaruco River. For the Cinaruco, all of the physicochemical, respiration and production estimates, except for turbidity, were available from a previous study (Cotner *et al.*, 2006). Turbidity in the Cinaruco River was measured from June 2011 to March 2012. In the Brazos, Tambopata, Guadalupe and Neches rivers, measurements were taken from May 2009 to February 2012.

For the Texas rivers, % bankfull discharge was estimated using mean daily stage height data from the United States Geological Survey (USGS, station 081087800 for the Brazos River, 08176500 for the Guadalupe River, 08041000 for the Neches River) and bankfull stage condition values from the National Weather Service. In the Tambopata River, % bankfull discharge was determined by measuring daily water level using a metre stick and by visually estimating periods when the river exceeded bankfull stage from the floodplain levee height. In the Cinaruco River, % bankfull discharge was estimated using measurements from Montoya *et al.* (2006). To measure nutrient concentrations, water samples were collected in acid-rinsed polyethylene bottles, filtered through a Whatman GF/F filter and analysed immediately using colorimetric assays and a Technicon II Autoanalyzer for the Cinaruco River and a Hach DR 2800 mass spectrophotometer for all other rivers (APHA, 1998). We report dissolved inorganic nitrogen (DIN) as the sum of NH_4, NO_2 and NO_3. A Hanna microprocessor turbidity meter was used to measure turbidity.

Light and dark chambers were used to estimate ecosystem R (the sum of autotrophic and heterotrophic R), NEP and gross primary production (GPP) of the water column and benthos following Cotner (2006). During incubations, a Hydrolab MiniSonde was placed near the chambers to record ambient water temperature (°C), pH, specific conductivity ($\mu S\ cm^{-1}$) dissolved oxygen (DO, $mg\ L^{-1}$) and salinity (ppt). Water-column measurements followed Wetzel & Likens (1991). Six 300-mL light and six dark biological oxygen demand (BOD) bottles were filled with water collected from 30 cm below the surface and incubated at approximately 1 m depth. Changes in DO concentration were measured with a YSI Model 85 DO probe. For benthic measurements, two light and two dark circular Plexiglass benthic chambers, each with a propeller to gently mix water, were pressed into the sediment to enclose the substratum and approximately 8 L of river water. Dissolved oxygen concentration was measured every 5 min with an internally logging Hydrolab MiniSonde. All light measurements were taken for 3–4 h during cloudless or partly cloudy weather conditions, and all dark chamber measurements were taken for 1.5 h so that DO concentrations did not decrease below ambient. Water-column fluxes in DO were subtracted from the total benthic chamber flux, resulting in sediment-only fluxes (Cotner *et al.*, 2006). A respiratory quotient of 0.8, and a photosynthetic quotient of 1.2, was used when converting data from O_2 to C. Benthic flux was calculated using the methods in Dollar *et al.* (1991). Daily measurements were averaged and multiplied by 24 h (for R) or 12 h (for NEP and GPP). Although other studies have used the terms 'autotrophic' and 'heterotrophic' to refer to whole ecosystems, here we use the terms to refer to our chamber measurements (i.e. autotrophic = positive [water-column + benthic NEP], heterotrophic = negative [water-column + benthic NEP]) that are scalable to river littoral zones. Before calculating water-column + benthic NEP, we multiplied water-column NEP by 1 m, the approximate depth of sample incubation.

For chlorophyll *a*, triplicate samples of water were collected in acid-rinsed polyethylene bottles and filtered through Whatman GF/C filters. Triplicate samples of sediment were collected using a small plastic Petri dish (5 cm diameter and 1.3 cm height) and a spatula at a depth of approximately 0.5 m. Filter and sediment samples were immediately placed into individual dark vials for extraction for 24 h using 90% ethanol. Chlorophyll *a* was measured spectrophotometrically and corrected for phaeophytin by subtracting absorbances after the addition of 0.1N HCl (Wetzel & Likens, 1991).

Data analysis

To determine water periods, we used historical stage height data (July 1993–December 2011 for the Brazos, February 1987–October 2011 for the Guadalupe, October 1991–November 2011 for the Neches and January 2002–July 2003 for the Cinaruco) and plotted % frequency versus mean bimonthly % bankfull discharge. The greatest difference in subsequent bins was used to distinguish between the low-water period and the high-water period. Historical stage height data were not available for the Tambopata River, so we used stage height data taken by Los Amigos Biological Station staff from the Madre de Dios River from August 2001–July 2004 at a location ca. 43 km from its confluence with the Tambopata River. We also tested whether time since last flow disturbance had an effect on algal production and biomass by counting the number of days prior to sample collections that % bankfull discharge was <50 in the Brazos, Guadalupe, Neches and Cinaruco rivers. We chose 50% bankfull discharge as a flow disturbance threshold because at this water level most point sandbars are submerged. Linear regressions indicated that number of days since flow event was significantly related to NEP only for the benthos in the Neches River ($R^2 = 0.30$, $P < 0.01$) and did not predict GPP in any of the rivers. The number of days since a flow event was significantly associated with chlorophyll *a* only in the Brazos River (water-column $R^2 = 0.28$, $P < 0.05$; benthic $R^2 = 0.27$, $P < 0.05$) and for the benthos in the Cinaruco River ($R^2 = 0.26$, $P < 0.05$). Thus, we used water period and % bankfull discharge for subsequent statistical analyses.

To explore the effect of hydrology on nutrient concentrations and autochthonous production, we used two-way repeated-measures ANOVAs to compare nutrients and algal production parameters (water-column and benthic NEP, GPP, and R and chlorophyll *a*) between the samples taken at the low-water and high-water periods. We treated multiple samples (daily means) as independent observations and used water period as the first factor and river as the second factor. The repeated-measures ANOVA nested ‘sandbank’ within ‘river’. When both variables were significant and no interaction effect was present, we used pairwise t-tests to examine differences among rivers. We transformed SRP values [$\log_{10}(x + 1)$] and DIN and silica values [$\log_{10}(x)$] before performing statistical analyses. Linear regressions and correlations were used to examine relationships between % bankfull discharge and turbidity, nutrients and water-column NEP and GPP, and turbidity and water-column NEP and GPP. When it was clear that linear models did not fit the data, regressions were determined using a logarithmic model. Finally, we used regression tree analysis (e.g. De’ath & Fabricius, 2000) to predict water-column and benthic GPP and chlorophyll *a* based on river identity, % bankfull discharge, temperature, turbidity and nutrients. We did not use a cross-validation procedure to prune trees because of the small size of our data set. When plotting trees, nutrient concentrations were back-calculated from log-transformed data to ease interpretation. Relationships between turbidity and production variables and regression tree analyses were not calculated for the Cinaruco River because samples were not taken on the same days. We used the software program R (R Core Team, 2013) for all statistical analyses and considered results with $P < 0.05$ to be statistically significant. We used the TREE library to generate regression trees (Ripley, 2007).

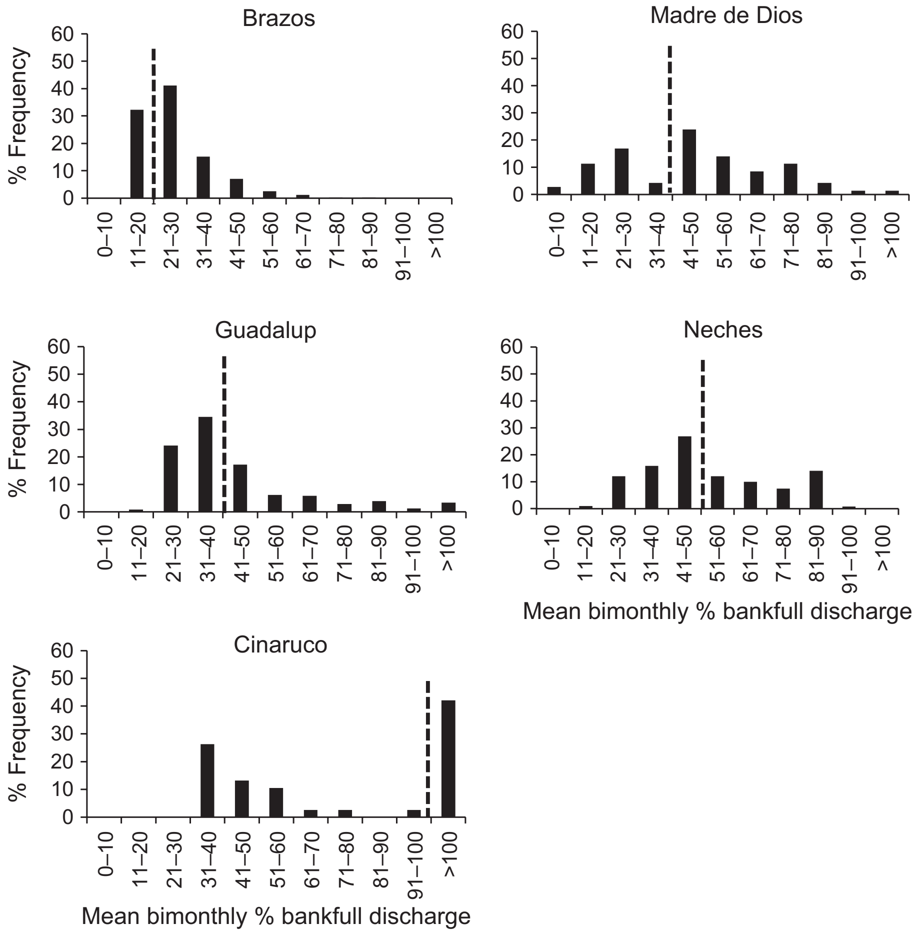

Fig. 2 Historical stage height data plotted as % frequency versus mean bimonthly % bankfull discharge for the study rivers. Historical stage height data were not available for the Tambopata River; therefore, data from the Madre de Dios River, of which the Tambopata River is a tributary, were used as a surrogate. Dotted line indicates the river stage used to distinguish low- and high-water periods. Note that historical flows include flows regulated by impoundments for the Brazos, Guadalupe and Neches rivers. Rivers are ordered by decreasing turbidity.

Results

Frequency histograms of mean bimonthly % bankfull discharge

Frequency histograms of % bankfull discharge were right-skewed for the Brazos and Guadalupe rivers, an indication that much of the annual flow is derived from high-flow pulses of short duration (Fig. 2). Frequency histograms for the Neches and Madre de Dios rivers (the latter characterising the hydrology of the Tambopata River) approached a normal distribution. In the Cinaruco River, a bimodal distribution was present, associated with the sinusoidal hydrological regime of this river consisting of annual low-flow and high-flow periods separated by gradual transitions. The difference in relative frequency between subsequent bins used to distinguish between hydrological periods was similar in magnitude among the Brazos, Tambopata, Guadalupe and Neches rivers, but higher for the Cinaruco River because of its sinusoidal flood pulse (Brazos = 26, Tambopata = 20, Guadalupe = 18, Neches = 15, Cinaruco = 39). In the temperate rivers, where mean daily discharge data were available, discharge during the low-water period averaged 39 $m^3 s^{-1}$ (range 4–150 $m^3 s^{-1}$) for the Brazos, 23 $m^3 s^{-1}$ (range 1–51 $m^3 s^{-1}$) for the Guadalupe and 69 $m^3 s^{-1}$ (range 8–136 $m^3 s^{-1}$) for the Neches. Discharge during the high-water period averaged 397 $m^3 s^{-1}$ (range 118–2390 $m^3 s^{-1}$) for the Brazos, 137 $m^3 s^{-1}$ (range 36–3256 $m^3 s^{-1}$) for the Guadalupe and 342 $m^3 s^{-1}$ (range 85–1161 $m^3 s^{-1}$) for the Neches.

Nutrients and turbidity

ANOVA indicated that differences between water periods were significant for SRP ($F_{1,126} = 13.69$, $P < 0.001$) and that SRP varied with river type ($F_{4,126} = 25.77$, $P < 0.001$). Differences in SRP between water periods depended on the river (interaction $F_{4,126} = 12.43$, $P < 0.001$). In the temperate (Texas) rivers, where land use was more intense, mean SRP was higher during the high-water period, whereas, in the tropical rivers, mean SRP was higher during the low-water period (Fig. 3). Concentrations of SRP also were higher in the temperate than in the tropical rivers. SRP concentrations in the Guadalupe River were particularly high, at times rivalling those typical of wastewater.

Differences between water period were significant for DIN ($F_{1,126} = 6.52$, $P < 0.05$) and DIN varied significantly among rivers ($F_{4,126} = 52.28$, $P < 0.001$). The interaction between water period and river was significant for DIN ($F_{4,126} = 2.85$, $P < 0.05$). Mean DIN was higher during the high-water period in the temperate rivers and during the low-water period in the tropical rivers (Fig. 3) and was higher in the temperate rivers than in the tropical rivers.

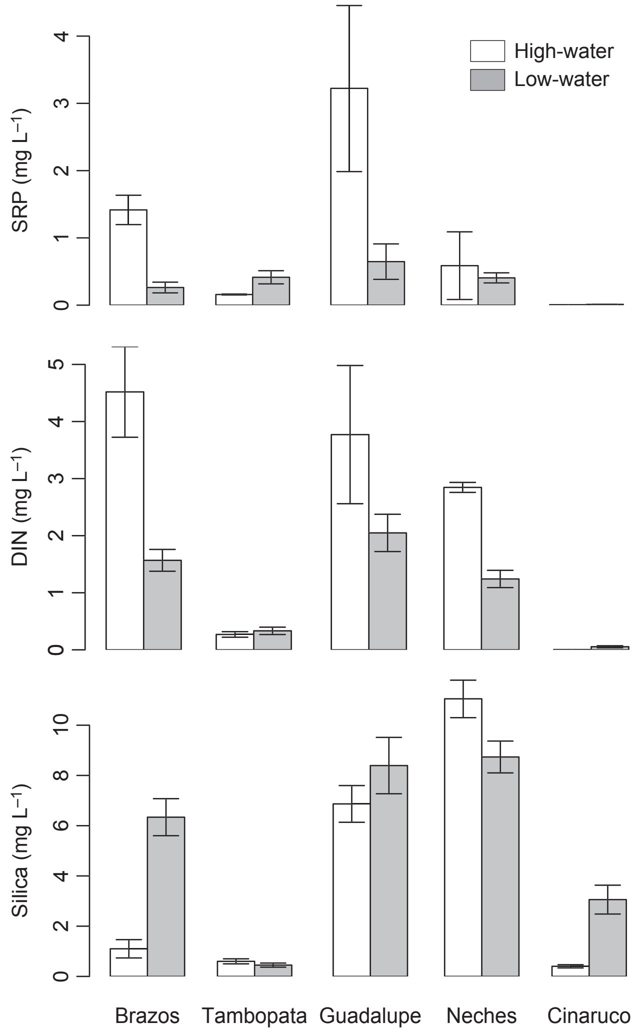

Fig. 3 Nutrient concentrations (mean ± SD in mg L^{-1}) measured during low- and high-water periods in each of the study rivers. SRP = soluble reactive phosphorus, DIN = dissolved inorganic nitrogen (the sum of NO_3, NO_2 and NH_4) and silica = SiO_3 in the Cinaruco River and SiO_2 in other rivers. Mean SRP in the Cinaruco River during the low-water period = 0.010 mg L^{-1} (±0.005) and during the high-water period = 0.008 mg L^{-1} (±0.007). Mean DIN in the Cinaruco River during the low-water period = 0.011 mg L^{-1} (±0.007) and during the high-water period = 0.006 mg L^{-1} (±0.003). Brazos $n = 18$, Tambopata $n = 12$, Guadalupe $n = 17$, Neches $n = 22$, Cinaruco $n = 53$. Rivers are ordered by decreasing turbidity.

Silica varied significantly between water periods ($F_{1,126} = 32.70$, $P < 0.001$) and among rivers ($F_{4,126} = 11.68$, $P < 0.001$). The interaction term between water period and river also was significant for silica ($F_{4,126} = 4.38$, $P < 0.01$). Hydrology did not cause consistent differences in silica concentrations between the temperate and tropical rivers (Fig. 3), although the temperate rivers had higher silica concentrations compared to the tropical rivers.

Turbidity was higher following periods of high flow in the sediment-laden rivers (i.e. Brazos and Tambopata) compared to the Guadalupe, Neches and Cinaruco rivers; in the Brazos and Tambopata rivers, flow pulses frequently produced turbidity in excess of 150 FTU (Brazos maximum = 1474, Tambopata maximum = 399), compared to a maximum of 367 FTU for the Guadalupe, 109 FTU for the Neches and 7.9 FTU for the Cinaruco (Fig. 4). Linear regression revealed that turbidity was positively associated with % bankfull discharge in both of the sediment-laden rivers (Brazos $R^2 = 0.64$, $P < 0.01$; Tambopata $R^2 = 0.84$, $P < 0.001$) and the Guadalupe River ($R^2 = 0.73$, $P < 0.001$). In the Neches River, turbidity increased only slightly following flow pulses, and thus, turbidity was not associated with discharge (linear regression, $R^2 = 0.15$, $P = 0.491$). In the Cinaruco River, turbidity was negatively associated with discharge because increased concentrations of humic substances and phytoplankton during periods of low flow reduced water clarity (linear regression, $R^2 = -0.84$, $P < 0.001$). The much smaller absolute differences in turbidity in the Neches and Cinaruco rivers than in the Guadalupe River and the sediment-laden rivers suggest that ecological implications of turbidity may not be detectable in the first two.

Respiration and production variables

ANOVA revealed that water period had no effect on water-column R ($F_{1,114} = 0.86$, $P = 0.36$; Fig. 5) or benthic R ($F_{1,71} = 0.18$, $P = 0.67$; Fig. 6) measured in littoral habitats. Differences among rivers were significant for water-column R ($F_{4,114} = 5.32$, $P < 0.001$), but not for benthic R ($F_{4,71} = 1.17$, $P = 0.33$).

Differences between water period were significant for water-column NEP ($F_{1,114} = 10.13$, $P < 0.01$; Fig. 5), but not for benthic NEP ($F_{1,71} = 1.50$, $P = 0.22$; Fig. 5). River had a significant effect on water-column NEP ($F_{4,114} = 10.39$, $P < 0.001$), but not on benthic NEP ($F_{4,71} = 0.45$, $P = 0.77$). There was no significant interaction between water period and river for water-column NEP. Water-column NEP was higher during the low-water period

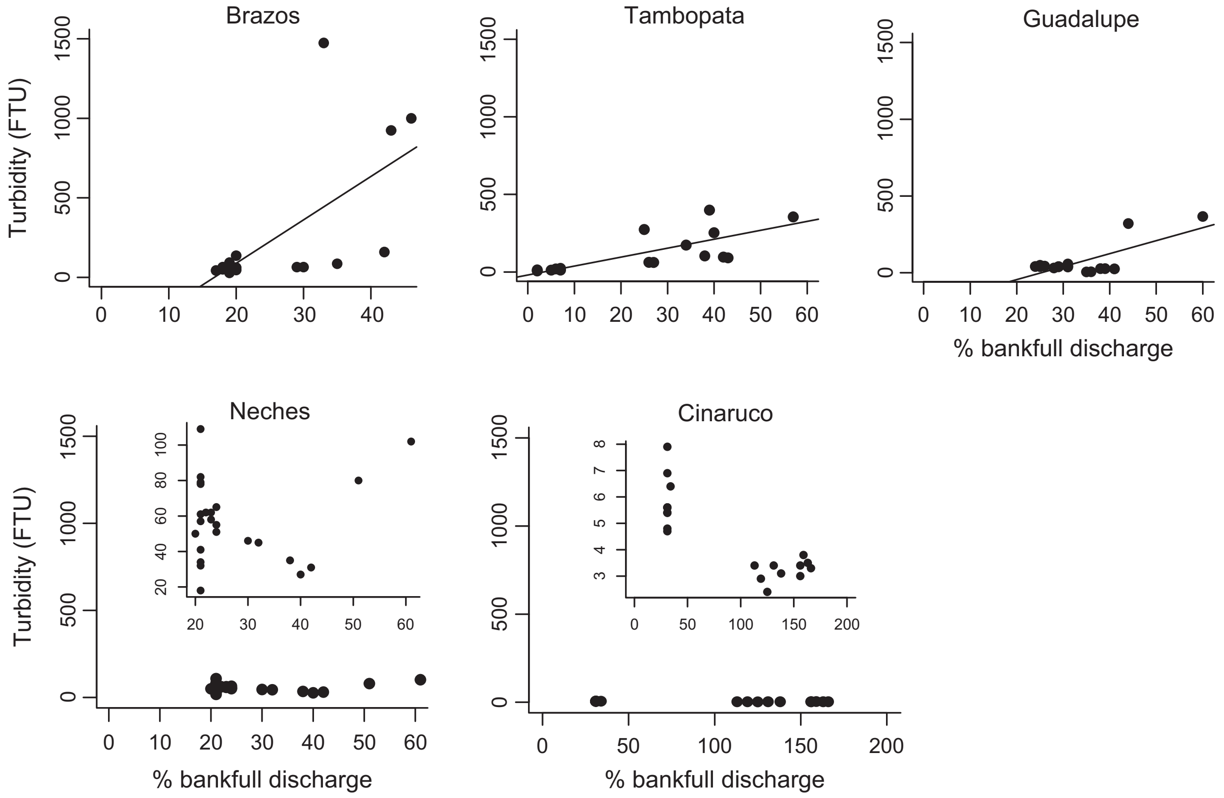

Fig. 4 Relationship between turbidity and % bankfull discharge in the Brazos, Tambopata, Guadalupe, Neches and Cinaruco rivers. Brazos *n* = 18, Tambopata *n* = 19, Guadalupe *n* = 17, Neches *n* = 24, Cinaruco *n* = 20. Regression lines are shown only for statistically significant relationships. Rivers are ordered by decreasing turbidity.

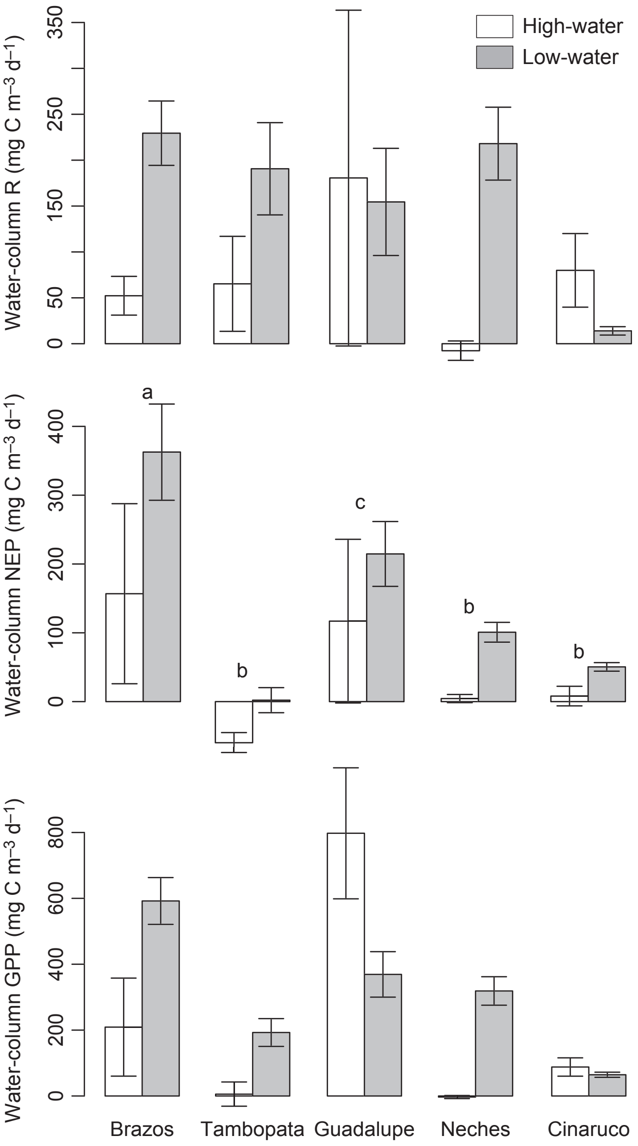

Fig. 5 Mean (±SD) water-column respiration (R), net ecosystem production (NEP) and gross primary production (GPP) during low- and high-water periods in five study rivers. Brazos n = 20, Tambopata n = 12, Guadalupe n = 17, Neches n = 22, Cinaruco n = 41. Rivers are ordered by decreasing turbidity. Please note that y-axis scales are variable.

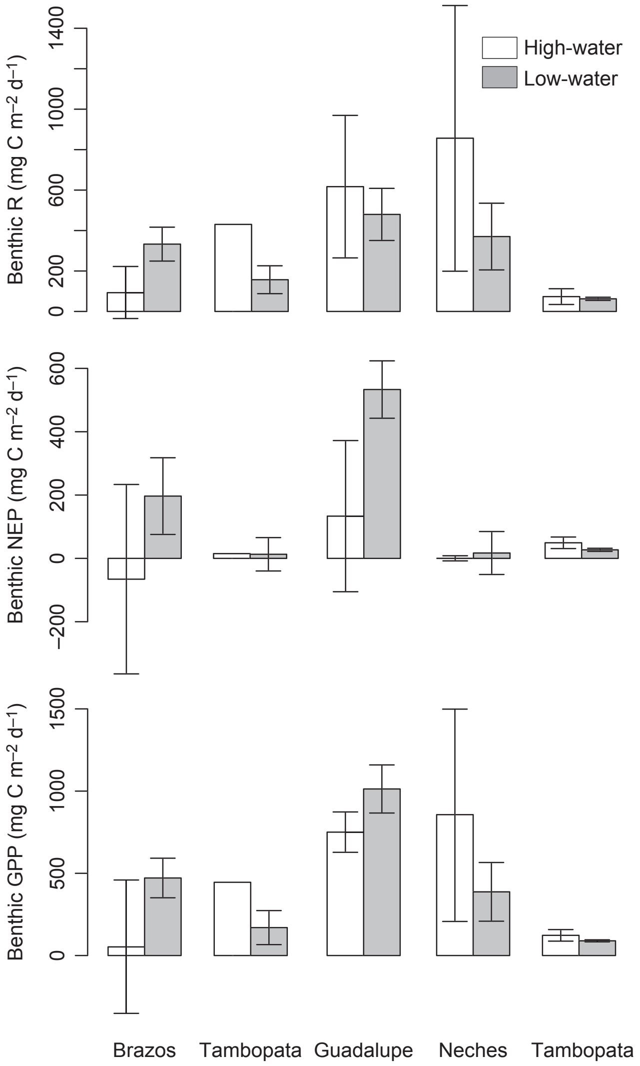

Fig. 6 Mean (±SD) benthic respiration (R), net ecosystem production (NEP) and gross primary production (GPP) during low- and high-water periods in the study rivers. Brazos n = 20, Tambopata n = 10, Guadalupe n = 17, Neches n = 22, Cinaruco n = 41. Rivers are ordered by decreasing turbidity.

than in the high-water period. Pairwise t-tests revealed three groups with significant differences in water-column NEP: the Brazos, the Guadalupe and the Tambopata + Neches + Cinaruco ($P < 0.05$).

Littoral zones in both of the sediment-laden rivers were heterotrophic following periods of high discharge, as indicated by negative total (water-column + benthic) NEP values. We sampled two periods when both water-column and benthic NEP in Brazos River littoral habitats were negative. For the first period (during May 2009), flooding of similar magnitude (25% bankfull discharge) had not occurred for >8 months. For the second period (during January/February, 2012), flooding of a similar magnitude (53% bankfull discharge) had not occurred for >16 months. In the Brazos River, values of total NEP were positive at a higher discharge than were negative measurements, but when littoral zones were autotrophic, flooding of a similar magnitude had occurred relatively recently. For example, in May 2010, the littoral zone was autotrophic at 42% bankfull discharge, but flooding of a similar magnitude had occurred <1 month earlier. In the Tambopata River, total NEP was consistently positive only after the water level fell below approximately 10%

bankfull discharge. In contrast, in the other study rivers, total NEP was almost always positive during both low- and high-water periods. In the Guadalupe and Neches rivers, the few occasions when the littoral zone was heterotrophic resulted from very negative benthic NEP values, probably caused by anaerobic processes in the sediments. In the Cinaruco River, littoral zone total NEP was consistently positive.

Differences between water period were not significant for water-column GPP ($F_{1,114} = 2.18$, $P = 0.14$; Fig. 5) or for benthic GPP ($F_{1,70} = 0.64$, $P = 0.43$; Fig. 6). Differences among study rivers were significant for water-column GPP ($F_{4,114} = 22.15$, $P < 0.001$), but not for benthic GPP ($F_{4,70} = 0.57$, $P = 0.69$). Unlike water-column NEP, ANOVA revealed a significant interaction term between period and river for water-column GPP ($F_{4,114} = 6.53$, $P < 0.001$). However, for all the study rivers, mean water-column GPP was consistently higher during low water.

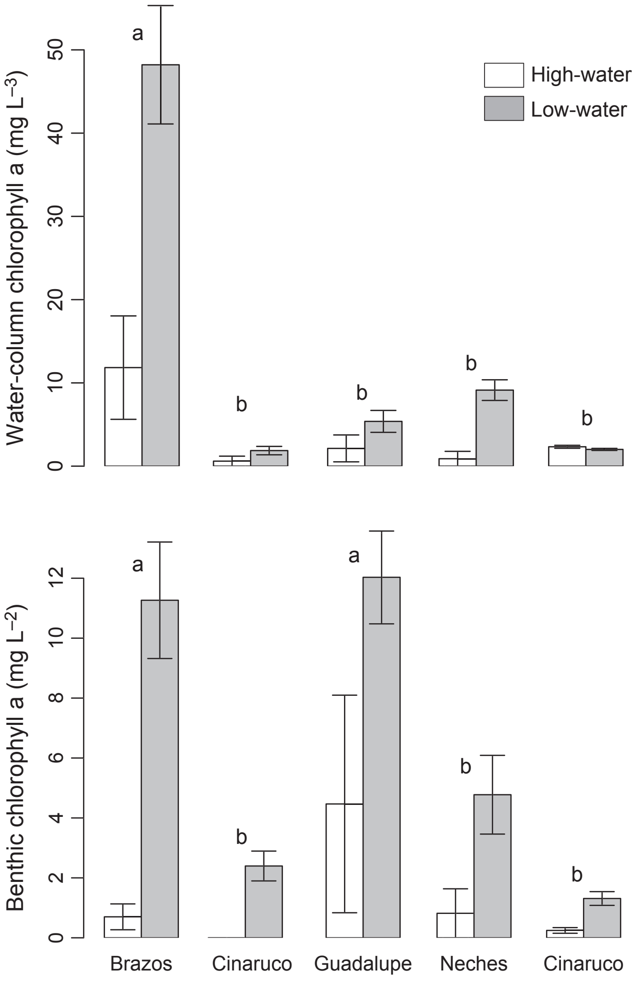

Fig. 7 Mean (±SD) water-column and benthic chlorophyll *a* (chlor *a*) during low- and high-water periods in the study rivers. Brazos $n = 18$, Tambopata $n = 8$, Guadalupe $n = 16$, Neches $n = 21$, Cinaruco $n = 28$. Letters indicate significantly different rivers. Rivers are ordered by decreasing turbidity.

ANOVA revealed significant differences between water period for both water-column chlorophyll *a* ($F_{1,74} = 24.36$, $P < 0.001$) and benthic chlorophyll *a* ($F_{1,74} = 16.62$, $P < 0.001$). Differences among rivers also were significant for both water-column chlorophyll *a* ($F_{4,74} = 20.60$, $P < 0.001$) and benthic chlorophyll *a* ($F_{4,74} = 2.70$, $P < 0.05$). The interaction term between water period and river was not significant for water-column chlorophyll *a* ($F_{4,74} = 1.90$, $P = 0.12$) or for benthic chlorophyll *a* ($F_{4,74} = 1.75$, $P = 0.15$). Mean water-column chlorophyll *a* was higher during the low-water period for every study river but the Cinaruco (Fig. 7). Benthic chlorophyll *a* was higher during the low-water period than in the high-water period (Fig. 7). Pairwise t-tests indicated that water-column chlorophyll *a* was significantly higher in the Brazos River than in any other study river and that benthic chlorophyll *a* was significantly higher in the Brazos and Guadalupe rivers than in the Tambopata, Neches and Cinaruco rivers ($P < 0.05$).

Associations between nutrients, turbidity and production variables

Linear regressions indicated that the only significant relationships between SRP, DIN and silica concentrations, and water-column NEP, were for the Brazos and Neches rivers. In both rivers, water-column NEP of the littoral zone was negatively associated with DIN (linear regression, Brazos $R^2 = 0.28$, $P < 0.05$; Neches $R^2 = 0.28$, $P < 0.05$). Associations between water-column NEP and SRP and DIN were similar among the temperate rivers. In all three temperate rivers, a reduction in water-column NEP was associated with increasing SRP and DIN (correlation, PCC for SRP, Brazos = -0.47, $P < 0.05$; Guadalupe = -0.44, $P = 0.07$; Neches = -0.29, $P = 0.19$; PCC for DIN, Brazos = -0.53, $P < 0.05$; Guadalupe = -0.37, $P = 0.15$; Neches = -0.53, $P < 0.05$).

The only significant relationships between water-column GPP and nutrients were for the temperate rivers. There, water-column GPP decreased with increasing SRP and/or DIN (linear regression for SRP, Brazos $R^2 = 0.37$, $P < 0.05$; linear regression for DIN, Brazos $R^2 = 0.45$, $P < 0.01$, Neches $R^2 = 0.35$, $P < 0.01$, Guadalupe $R^2 = 0.48$, $P < 0.01$). Again, correlations indicated that associations between water-column GPP and SRP and DIN were similar among the three temperate rivers. In the three temperate rivers, water-column NEP was negatively associated with SRP and DIN (PCC for SRP, Brazos = –0.62, $P < 0.01$; Guadalupe = –0.37, $P = 0.14$; Neches = –0.35, $P = 0.11$; PCC for DIN, Brazos = –0.67, $P < 0.01$; Guadalupe = –0.69, $P < 0.01$; Neches = –0.59, $P < 0.01$).

The negative associations between SRP and DIN and water-column production variables in the three temperate rivers were likely to be partly a result of limitation of algal primary production by low water temperature during periods of high nutrient concentrations. In the temperate rivers, high discharge occurred during the spring and thus was negatively associated with water temperature (Brazos PCC = –0.46, $P = 0.05$; Guadalupe PCC = –0.60, $P < 0.05$; Neches PCC = –0.39, $P = 0.07$). Linear regressions revealed a significant relationship between water-column NEP and water temperature in the Tambopata ($R^2 = 0.48$, $P < 0.05$), Guadalupe ($R^2 = 0.40$, $P < 0.01$) and Neches ($R^2 = 0.27$, $P < 0.05$) rivers. Correlations indicated that water-column NEP was typically higher at higher water temperature in the Cinaruco River as well (PCC = 0.40, $P = 0.06$). Water-column GPP was significantly positively associated with water temperature in the Neches River (linear regression, $R^2 = 0.48$, $P < 0.001$) and Guadalupe River (linear regression, $R^2 = 0.69$, $P < 0.0001$), and water-column GPP tended to be greater at higher water temperatures in the Brazos (PCC = 0.43, $P = 0.08$) and Cinaruco (PCC = 0.39, $P = 0.06$).

Logarithmic regressions provided the best fit for relationships between turbidity and production variables. Logarithmic regressions indicated that increasing turbidity was significantly associated with a reduction in water-column NEP in the Brazos ($R^2 = 0.50$, $P < 0.01$), the Tambopata ($R^2 = 0.55$, $P < 0.01$) and Neches ($R^2 = 0.35$, $P < 0.01$; Fig. 8). Water-column GPP was significantly negatively associated with turbidity only within the Brazos River (logarithmic regression, $R^2 = 0.59$, $P < 0.001$).

Regression tree analysis

The water-column GPP regression tree model revealed nine nodes and a residual mean deviance of 29 200. Among all potential predictor variables, river, temperature, DIN and silica were used in model construction. Temperature caused the primary split, with low temperature resulting in lowest water-column GPP values (Fig. 9). The secondary split was between the Tambopata and Neches rivers, which generally had lower water-column GPP, and the Brazos and Guadalupe rivers, which

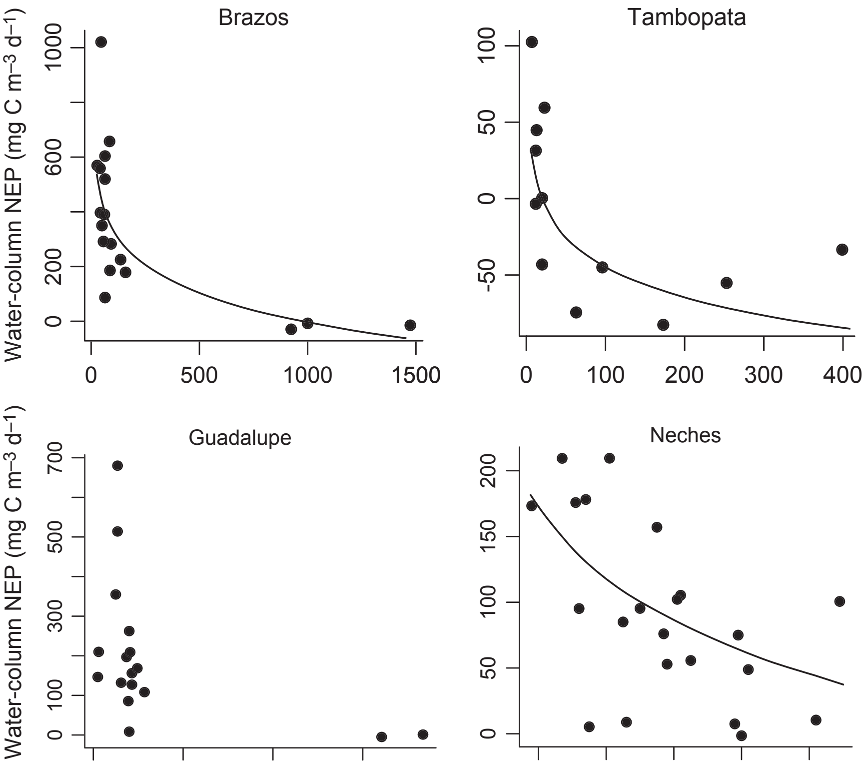

Fig. 8 Relationship between water-column net ecosystem production (mg C m^{-3} day^{-1}) and turbidity (FTU) in the Brazos, Tambopata, Guadalupe and Neches rivers. Brazos $n = 18$, Tambopata $n = 12$, Guadalupe $n = 17$, Neches $n = 22$. Data for the Cinaruco River are not available. Regression lines are shown only for statistically significant relationships. Rivers are ordered by decreasing turbidity.

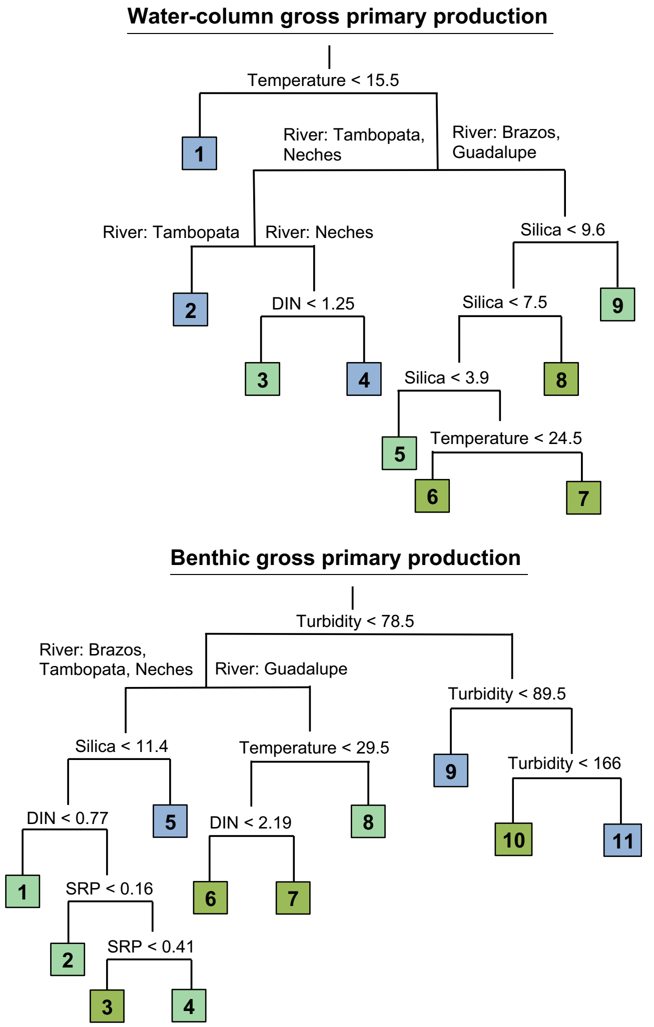

Fig. 9 Water-column and benthic gross primary production (GPP) regression tree models. Each split in the tree is labelled with the variable and an inequality that determines the split. If the inequality is true, advance to the left branch. Each of the nodes is numbered. A green node indicates that GPP is high, and a blue node indicates that GPP is low.

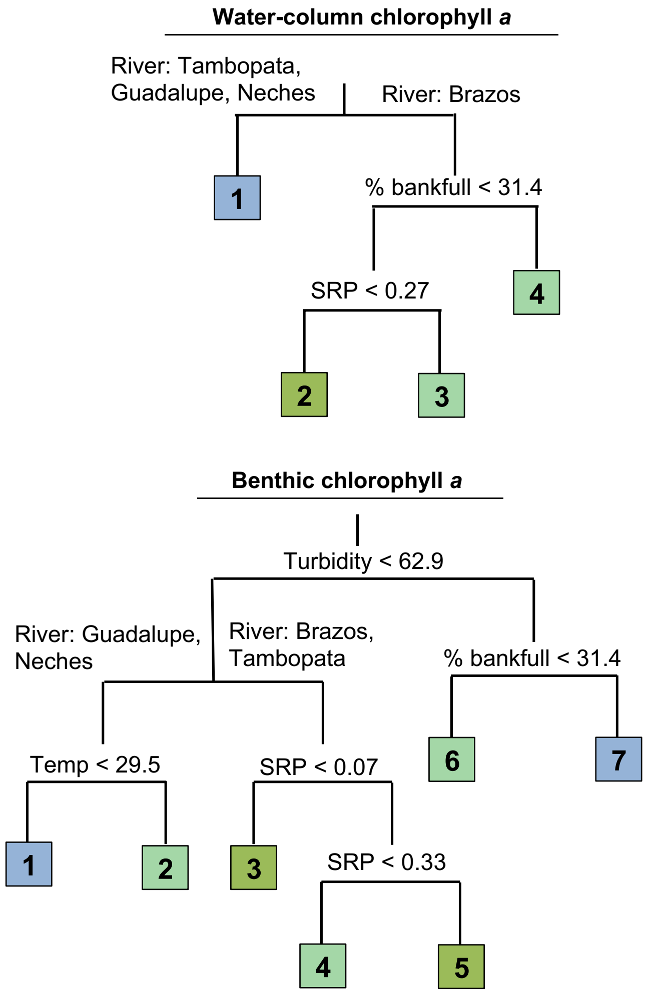

Fig. 10 Water-column and benthic chlorophyll *a* regression tree models. Each split in the tree is labelled with the variable and an inequality that determines the split. If the inequality is true, advance to the left branch. Each of the nodes is numbered. A green node indicates that chlorophyll *a* is high, and a blue node indicates that chlorophyll *a* is low.

had higher water-column GPP. The benthic GPP tree was the most complex, with 11 nodes and a residual mean deviance of 202 000. Variables used in model construction included river, temperature, turbidity, SRP, DIN and silica. In the benthic GPP model, turbidity caused the primary split, with high turbidity values largely associated with low benthic GPP, but also some high benthic GPP values in the Brazos River (Fig. 9).

The water-column chlorophyll *a* regression tree model had four nodes and a residual mean deviance of 130. Only river, % bankfull discharge and SRP were used in tree construction. The water-column chlorophyll *a* regression tree revealed a primary split between the Tambopata, Guadalupe and Neches rivers and the Brazos River (Fig. 10). In the Brazos River, % bankfull discharge and SRP caused additional splits. The benthic chlorophyll *a* model had seven nodes, and five variables were used in model construction: river, % bankfull discharge, temperature, turbidity and SRP (residual mean deviance 18.5). In the benthic chlorophyll *a* model, turbidity caused the primary split and % bankfull discharge and river caused secondary splits (Fig. 10).

Discussion

Our main objective was to investigate factors influencing aquatic primary production in shallow littoral zones of rivers with varying physicochemical characteristics.

Table 2 Hypothesised and actual responses of autochthonous primary production in littoral zones to flow, nutrients and turbidity in the five study rivers

	Hypothesised response		Actual response	
Study river	Low water	High water	Low water	High water
Brazos	Autotrophic	Heterotrophic	Dependent on frequency and duration of hydrology	
Tambopata	Heterotrophic	Heterotrophic	Autotrophic	Heterotrophic
Guadalupe	Autotrophic	Autotrophic	Autotrophic	Autotrophic
Neches	Autotrophic	Autotrophic	Autotrophic	Autotrophic
Cinaruco	Autotrophic	Autotrophic	Autotrophic	Autotrophic

Our measurements of respiration and primary production in littoral habitats cannot be scaled to an entire river because contributions of other spatial compartments (e.g. deep channel, ground water) would need to be estimated. Because of their limited depth and low current velocity, littoral habitats have been hypothesised to be particularly important areas for the production of benthic algae that support aquatic food webs (Thorp & Delong, 1994; Hein *et al.*, 2005). Littoral habitats are important feeding areas for common and diverse macroinvertebrates and fishes (Arrington & Winemiller, 2003; Winemiller *et al.*, 2006; Roach & Winemiller, 2011). We originally expected that interactions between flow, nutrients and turbidity would influence autochthonous production in littoral zones of the sediment-laden Brazos River (Table 2). At high river discharge, we expected littoral zones to be heterotrophic, while, at low river discharge, we anticipated high algal production and biomass. We expected relatively little algal production and biomass in the sediment-laden Tambopata River regardless of flow, because of low concentrations of inorganic nutrients. In the Guadalupe, Neches and Cinaruco rivers, we expected littoral zones to be autotrophic at both low and high river discharge, because soils are less dispersive (erodible) and thus transparency remains relatively high during periods of high flow.

Interactions among hydrology, turbidity and nutrient concentrations had greatest influence on instream primary production in shallow littoral zones of rivers with highly erodible fine sediments, such as the Brazos River. In the Brazos, NEP and chlorophyll *a* values were much lower following high-flow pulses. Following an extended period of low flow during June 2011, water-column NEP was 292 mg C m^{-3} day^{-1}, water-column GPP was 557 mg C m^{-3} day^{-1} and water-column chlorophyll *a* was 35 mg m^{-3}. Following a flow pulse in January 2012, water-column NEP was −30 mg C m^{-3} day^{-1}, water-column GPP was 32 mg C m^{-3} day^{-1} and water-column chlorophyll *a* was 2 mg m^{-3}. In the Tambopata River, NEP and chlorophyll *a* values were reduced during the annual high-water period as a result of low water transparency and low inorganic nutrient concentrations. During the annual low-water period, transparency increased and NEP was probably limited by low concentrations of inorganic nutrients. Water-column NEP in the Tambopata River peaked at 103 C m^{-3} day^{-1} (water-column GPP = 108 mg C m^{-3} day^{-1}, peak water-column chlorophyll $a = 3$ mg m^{-3}) during the low-water period in August. During the high-water period, water-column NEP was <-40 mg C m^{-3} day^{-1} and chlorophyll *a* ranged from 0 to 2 mg m^{-3}.

In some of the temperate rivers, nutrient concentrations were higher during brief spates (i.e. SRP and DIN in the Brazos River and DIN in the Neches River). In contrast, in the tropical rivers, dissolved inorganic nutrient concentrations tended to be higher during the annual low-water period (i.e. SRP in the Tambopata and DIN in the Cinaruco). Many studies have found that, in temperate rivers, nutrient concentrations are highest following peak flows, particularly if flooding is preceded by a long period of low flow (Fisher & Minckley, 1978; Mitsch *et al.*, 2001; Doyle *et al.*, 2005). Conversely, in tropical rivers, nutrient concentrations are frequently highest during the annual low-water period (Lewis, 1988; Castillo, 2000; Cotner *et al.*, 2006). Riverine solutes arise from the atmosphere, weathering, anthropogenic sources or recycling of organic material. Increased nutrient concentrations that follow flooding in temperate rivers may be a result of greater weathering in temperate compared to tropical catchments that are frequently highly leached (Allan, 1995). Additionally, agriculture and cattle grazing is common within the basins of all three Texas study rivers. Extended periods without precipitation allow nutrients from fertiliser and livestock to accumulate along river banks and other areas within catchments; subsequent rainfall results in high nutrient concentrations in run-off. Farmers within the Tambopata Basin typically practise shifting cultivation and small-scale cattle production solely for local subsistence (Foster *et al.*, 1994). In the Cinaruco Basin, soils are oligotrophic with a high quartzite (silica) content (Sarmiento & Pinillos, 2001); consequently, very little agriculture is practised in this region. Presumably, because anthropogenic nutrient sources were relatively minor within the two tropical river basins studied here, dilution reduces dissolved nutrient concentrations during extended periods of high discharge. Despite the different patterns in seasonal nutrient concentrations, our instream production and chlorophyll *a* measurements indicated that, in all the rivers, algal production is usually higher during periods of low discharge, probably because of the lack of flow pulses that scour algal cells, higher nutrient concentrations within the tropical rivers and, in the cases of the rivers with fine sediments (Brazos, Tambopata, Guadalupe), lower turbidity. In the temperate rivers, increased nutrient concentrations during periods of high flow are unlikely to have a positive effect on algal production and biomass, because nutrients were consistently above values required for algal growth (Hecky & Kilham, 1988).

In the two rivers that carried the highest loads of fine suspended sediments (Brazos, Tambopata), the NEP of littoral zones was negative (heterotrophic) during periods of high discharge, whereas in the Guadalupe, Neches and Cinaruco rivers, NEP in littoral zones was almost always positive, indicating that the littoral zone was autotrophic. In the Brazos River, in addition to discharge, the frequency and duration of flow events also explained NEP. Littoral habitats were heterotrophic during turbid, high-flow events that followed prolonged periods of low flow. In temperate rivers and streams, it is well established that the concentration of particles in the water-column depends not only on the discharge but also on the period since similar flows had occurred (Cummins *et al.*, 1983; Meyer, 1990; Doyle *et al.*, 2005). In the Tambopata River, dissolved nutrient concentrations were much lower, and flooding patterns more seasonal, than in the Brazos River, and consequently, the littoral zone was consistently heterotrophic above about 10% bankfull discharge.

Water-column and benthic R did not appear to have strong seasonal patterns, and seasonal differences among the rivers were not consistent. Because instream production did exhibit consistent patterns with water period, lack of a seasonal pattern in R may have occurred because heterotrophic respiration was greater than autotrophic respiration in our study rivers. Bacteria are frequently limited by organic carbon (e.g. Vallières *et al.*, 2008), and thus, interactions between the river channel and floodplain may better explain patterns in R than comparison between low- and high-water periods. Concentrations of particulate organic carbon in water columns often peak during the descending phase of a major flow pulse, when floodplain wetlands are drained, and also following floodplain inundation during the ascending phase, when labile organic matter from terrestrial vegetation leaches into the water (e.g. Depetris & Kempe, 1993). Studies have documented high rates of bacterial respiration in rivers during floodplain inundation (Richey *et al.*, 1980).

Although we did not observe a consistent seasonal pattern in R among the five rivers, we did observe relatively consistent seasonal patterns in NEP and chlorophyll *a*. In all five rivers, water-column NEP was higher at low discharge. Although water period did not have a significant effect on benthic NEP, mean benthic NEP was higher during low-discharge periods in every river except the Cinaruco. Mean water-column chlorophyll *a* was higher during low-discharge periods in every river but the Cinaruco, and in all five cases, mean benthic chlorophyll *a* was consistently higher at low discharge. Highest instream production has been shown to occur during the period of lowest river discharge in many other tropical river systems (e.g. Lewis, 1988; Castillo, 2000; Cotner *et al.*, 2006; Hunt *et al.*, 2012). In temperate rivers, because flow, nutrient concentrations and turbidity can exhibit substantial seasonal variation, the length of time since the last flood also explains variation in NEP. For example, in the Thur River in Switzerland, variation in GPP measured over a 15-year period primarily reflected time since the last spate and subsequent recovery, which influences light conditions and nutrient concentrations (Uehlinger, 2006). Moreover, recovery of GPP varied significantly with season and was faster during the months with highest temperature and greatest solar radiation (Uehlinger, 2006).

Other studies have highlighted the importance of shallow 'areas of retention' for plankton production (Reynolds & Descy, 1996; Reckendorfer *et al.*, 1999). During low-water periods, when the river channel is not hydrologically connected to aquatic habitats of the floodplain, retention areas in the riverscape should be major sources of primary production supporting primary consumers. For example, in some rivers dominated by fine sediments, including Cooper Creek in Australia and the Rio Grande in the United States, researchers have noted that during periods of low flow, algal growth is limited to shallow edges of the river channel and backwaters (Bunn *et al.*, 2003; Turner & Edwards, 2012). During periods of high discharge, when the main channel is hydrologically connected to off-channel slackwater habitats, high-quality organic matter can be exported from secondary channels or floodplain habitats to the river channel, and this material has been hypothesised to be a source of organic carbon for aquatic invertebrates and fish (Hein *et al.*, 2003; Zeug & Winemiller, 2008). In the Austrian reach of the River Danube, where the channel has a braided geomorphology, algal production originating from slow-flowing side channels is transported to the main channel during high-flow pulses (Hein *et al.*, 2003). In Australian rivers, fish migrate between floodplains and river channels resulting in net importation of production from the former to the latter, particularly in rivers where floodplains are inundated for long periods of time (Jardine *et al.*, 2012a,b).

All five of our study rivers have meandering single channels. The Cinaruco River is the most spatially heterogeneous, with numerous side channels and floodplain lagoons, most of which are hydrologically connected to the river channel during the annual flood pulse. Sloughs, side channels and other floodplain depressions also are present at our study site in the Neches River and, because of their low height, many are hydrologically connected to the river channel below bankfull stage height (e.g. Phillips, 2011). At our study sites in the Brazos, Tambopata and Guadalupe rivers, there are few slackwater habitats aside from oxbow lakes and shallow in-channel areas. In the Brazos River, hydrology is highly variable and unpredictable, and therefore, most oxbows are only briefly connected to the main channel at very high flow (Zeug & Winemiller, 2008). Because of the comparatively higher slope at our study site in the Tambopata River, water infrequently inundates the floodplain (Hamilton *et al.*, 2007). Thus, in the Brazos and Tambopata rivers, algae that are washed from oxbow lakes to the river channel seem unlikely to be a substantial source of labile organic matter in the river channel. Based on analysis of stable isotope data, Zeug and Winemiller (2008) concluded that fish inhabiting the main channel of the Brazos River assimilated larger fractions of material from terrestrial plants following a period of frequent hydrological connection between the river channel and oxbow lakes.

Based on currently available findings, aquatic consumers in most river systems appear to derive a large fraction of their organic matter from local autochthonous production (Hamilton, Lewis & Sippel, 1992; Thorp & Delong, 2002; Roach, 2013). If this indeed is the case, our results have strong implications for understanding river food web structure and predicting dynamics. In rivers that carry high loads of fine sediments, particularly those of low gradient and meandering geomorphology, terrestrial-based production may be more likely to support the food web following the peak flows that greatly limit autochthonous production in the main channel. To test this hypothesis, research using stable isotopes could estimate the relative importance of basal resources supporting the biomass of aquatic animals during different hydrological periods. Our study emphasises the need to understand how interactions among abiotic environmental variables, especially hydrology, suspended sediment load and nutrient concentrations, determine availability of alternative carbon sources supporting river food webs.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Sample dates and raw physicochemical data from the Brazos, Tambopata, Guadalupe and Neches rivers.

Appendix S2. Sample dates and raw production data from the Brazos, Tambopata, Guadalupe and Neches rivers.

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