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Original Research Article

Unraveling the ecological functioning of the monsoonal Songkhram river floodplain in Thailand by integrating data on soil, water, and vegetation

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ABSTRACT

Although the functioning of river floodplains as sink or source of nutrients has been studied extensively for temperate regions, similar studies in tropical regions are less abundant and studies integrating data about floodplain soil, vegetation, and water are scarce. We examined and compared nutrient contents in soil, water, and vegetation tissue in two different vegetation zones on the monsoon Songkhram river floodplain (Thailand). Significant differences were found between bamboo and grass zones. The soil in the bamboo zone is more fertile than the soil in the grass zone, as indicated by the lower C/N ratio, and has significantly higher organic matter and higher total N and K. Bamboo leaf tissue had significantly higher concentrations of nutrients than grass biomass. The growth of the bamboo is P-limited or P and N co-limited, but grass is N-limited. In both zones, the soil-available P and organic carbons after flooding were significantly lower than before flooding. Floodwater in both zones had low dissolved solid concentrations. After the flood peak, most concentrations tended to increase, especially organic carbon and dissolved nitrogen but phosphorus decreased. The results suggest a significant loss of organic carbon from the soil after flooding, indicating that the floodplain acts as a source of carbon that is exported downstream. Nonetheless it is also evident that the floodwater brings in sediment and nutrients. Based on rough estimations of nutrient budgets we conclude that the highly productive bamboo zone adjacent to the river filters out the nutrients before they reach the grass zone.

1. Introduction

River floodplains have been studied by wetland scientists for decades, since they represent ecosystems with valuable services to mankind. Understanding their hydrological and ecological functioning adds to insight into their key processes and how to preserve and protect them. The relevance of preservation of floodplains goes beyond the actual floodplain itself, since floodplains are typical connecting elements in the landscape between the hinterland and the river and also connect upstream areas with downstream areas. Due to this landscape connectivity, river floodplains harbor longitudinal and lateral gradients (Humphries et al., 2014; Junk and Wantzen, 2004; Vannote et al., 1980), and both vegetation productivity in floodplains and nutrient processes are related to the size of the parent river and its water quality (Spink et al., 1998; Thorp and Delong, 1994). It is therefore important to study floodplain processes further, to understand how these processes are linked to spatial

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zonation in the floodplain, upstream areas, and their distance from the river.

The hydrology and topography of floodplains largely determine their water flow, the development of gradients, and the existence of zones with different biological communities. Two other important factors that determine nutrient cycling in these communities are temperature and hydrochemistry. Floodplain hydrochemistry depends on the sources of inundation water: the principal sources are river water, groundwater, and precipitation, or mixtures of these. River floodwater is generally a source of nutrients (suspended and dissolved) (Mertes, 1997; Venterink et al., 2006; Wassen et al., 2003). Gradients in flood stress (e.g., depth, current velocity and oxygen stress during long-term inundations) and different magnitudes of nutrient and sediment inputs bring about spatial differentiation in productivity which, together with nutrient cycling processes result in distinct vegetation patterns in temperate floodplains (Keizer et al., 2014; Wassen et al., 2003; Wassen and Joosten, 1996; Wu and Blodau, 2015). Similar to the temperate floodplains, clear vegetation zonation along flooding gradients are observed in large tropical floodplains around the world i.e. the Amazon basin, the Okavango delta, the Mekong Tonle Sap and the tropical Northern Australia wet-dry system (Parolin et al., 2016; Parolin and Wittmann, 2010). Spatial patterns of vegetation in these tropical floodplains are the result of their adaptation and response to seasonally flooding characteristic, especially depth and duration (Arias et al., 2016; Parolin et al., 2016). Although each individual floodplain can have additional factors that influence the development of zonation such as interactions between soil, surface water and groundwater affecting the salinity in the Okavango floodplain (Ellery et al., 1993; Ellery and Tacheba, 2003), the effect on soil moisture due to disturbances from humans and fire in the Mekong Tonle Sap (Arias et al., 2013) and changing stream velocities during flood in the Northern Australia wet-dry tropics (Finlayson, 2005; Finlayson et al., 1990). In addition, nutrient availability in floodplains is an important factor as it determines the productivity of the floodplains. Spatial patterns of nutrient availability can directly cause vegetation zonation but can also influence seedling establishment strategies which result in spatial patterns of vegetation in floodplains (Parolin, 2002).

Crucial factors that determine nutrient dynamics and floodplain productivity are the hydrological regime and geochemical characteristics of the catchment (Spink et al., 1998). The hydrological regime may be characterized by three main river discharge stages; 1) a base flow stage 2) a rising stage and 3) the falling stage, as described in the river wave concept (Humphries et al., 2014) and flood pulse concept (Junk and Wantzen, 2004). During the base flow stage, the river and the floodplain are in a stage of low connectivity. During intense rainfall, the resulting terrestrial runoff not only causes water levels in the river channel to rise (the rising stage), but also transports dissolved and particulate nutrients. When the river overtops its banks, water from the river channel will inundate the floodplain, importing nutrients. At that moment, an aquatic system establishes on the floodplain and the floodwater transports suspended matter, dissolved solids, and propagules. The transport distance and the sedimentation rate are both a function of water velocity and floodplain topography, and they lead to a spatial redistribution of matter and organisms (Ward et al., 2002; Wiens, 2002; Zuijdgeest et al., 2015). Floodplain productivity is determined by the biomass production of phytoplankton, macro algae, aquatic plants, and helophytes. The major source of nutrients for aquatic production during the inundation phase is thought to be floodwater, with the floodplain soil playing a minor role, and thus when water stops overtopping the river banks, the supply of nutrients diminishes, as do nutrient concentrations in the floodwater (Lewis et al., 2000). In turn, floodplains can be an important source for organic carbon exported downstream via the river after the floods retreat (Junk and Wantzen, 2004; Zuijdgeest et al., 2015).

To date, most of the studies on the nutrient cycling processes occurring in floodplains have been on temperate systems e.g. (Baldwin and Mitchell, 2000; Venterink et al., 2003, 2002; Wassen et al., 2003). They have shown that river floodplains can function as a sink for nutrients such as N and P, and for sediment. Since both biomass production and organic matter decomposition depend greatly on temperature (Baldwin and Mitchell, 2000), it can be expected that there will be a clear difference in these processes between temperate catchments and tropical catchments. River floodplains in tropical regions may therefore be very different from temperate regions. McJannet et al. (2012) showed that a tropical floodplain was a sink for phosphorus but found no evidence for a nitrogen sink. Most studies in tropical river floodplains have analyzed the relationship between soil characteristic, hydrology and vegetation structure and composition (e.g. Arias et al., 2013; Finlayson, 2005; Murray-Hudson et al., 2011; Wittmann et al., 2008), and to some extent the hydrochemistry e.g. Ellery et al. (1993). Vegetation community patterns in tropical floodplains show clear correlations with flood characteristics such as flood duration and flood depth. Arias et al. (2016) demonstrated in their recent hydrogeological concept for vegetation distribution in tropical floodplains that a lower species diversity was found with longer flood duration and larger flood depth. Beside the relationship between flooding and vegetation types, flood characteristics also influence soil properties and nutrient contents (e.g. Arias et al., 2013).

However, little is known about the rate of nutrient cycling in tropical floodplains and how this relates to seasonal dynamics. Tropical monsoon rivers in particular exhibit a strong seasonal dynamic hydrologic pattern. The large amounts of rain characteristic in the monsoon period lead to low concentrations of dissolved matter and nutrients in river water during floodplain inundation (Walalite et al., 2016). However, similar to temperate floodplains, monsoon floodplains may show a distinct zonation of more productive and less productive vegetation (Arias et al., 2016; Walalite et al., 2016; Zuijdgeest et al., 2015). In the present study, we contribute to the sparse knowledge on tropical monsoon floodplain ecological functioning by presenting data on the Songkhram river in Thailand. Our two aims are: to explore spatial differences in nutrient distribution in water, soil, and vegetation for two distinct vegetation zones in the floodplain (bamboo and grass), and to understand the interaction between the flood characteristics and the vegetation with respect to nutrient fluxes and stores. In a previous study (Walalite et al., 2016), we identified two major vegetation communities that dominate in the floodplain: a bamboo zone that is widespread throughout the floodplain in a belt close to the river, and a grassland type behind the bamboo zone and thus further away from the river. In our earlier paper, we hypothesized that the high annual biomass production of the bamboo zone is driven by the floods importing nutrients and sediment and we urged for further research to analyze nutrient input and uptake in the grass and the bamboo zone. The present paper aims to verify this hypothesis and test if the less productive grassland zone behind the bamboo does indeed receive less input of nutrients from the river.

2. Study area

The Songkhram river catchment is situated in the monsoon climate region of north-eastern Thailand (Fig. 1). It is approximately 495 km long, drains an area of 13,000 km^2 and its average discharge is 226 m^3 s^{-1} during the monsoon season and 2.3 m^3 s^{-1} during the dry season. Annual precipitation averages 1960 mm and ranges from 1090 to 2880 mm. The monsoon season lasts from May to September and is followed by a cool dry season from October to February that is succeeded by a hot dry season from March to April. During the monsoon season the average precipitation is 1690 mm (range 906–2420 mm); this compares with an average precipitation of 270 mm (range 80–490 mm) during the dry season (figures compiled from daily data from the Department of Water Resources, Thailand). Mean annual daily temperature is 26 °C and the warmest month is April (monthly mean of 35 °C). From December to January the minimum night temperature is around 15 °C.

The floodplain we studied lies in the lower catchment of the Songkharam river (Fig. 1) and is inundated yearly due to the high river discharges during the monsoon season. The average flooded area of this floodplain is estimated to be 760–855 km^2 (Thiha et al., 2012; Walalite et al., 2016). The land uses of the flood-prone area in the non-flood season are agriculture (52%), grassland, herbaceous vegetation and shrubs (together 20%), open water (9%), marsh (8%) deciduous forest (6%), native riparian bamboo (4%) and buildings (1%).

The native floodplain vegetation community, which is known as "Pa Bung Pa Taam" (Fig. 2), comprises a distinct strip of dense thorny bamboo (*Bambusa flexuosa*) next to the river channel, behind which is a zone of grassland communities dominated by *Miscanthus fuscus* (Blake et al., 2011; Walalite et al., 2016). Fig. 3 presents a conceptual cross-section from the river across the floodplain to the higher non-flooded land on the side of the river valley, showing the zonation of bamboo and grass communities.

3. Methods

3.1. Sampling locations and time line of fieldwork campaign

We established four transects in the monsoon floodplain of the Songkhram river (Fig. 1). Each transect started on the

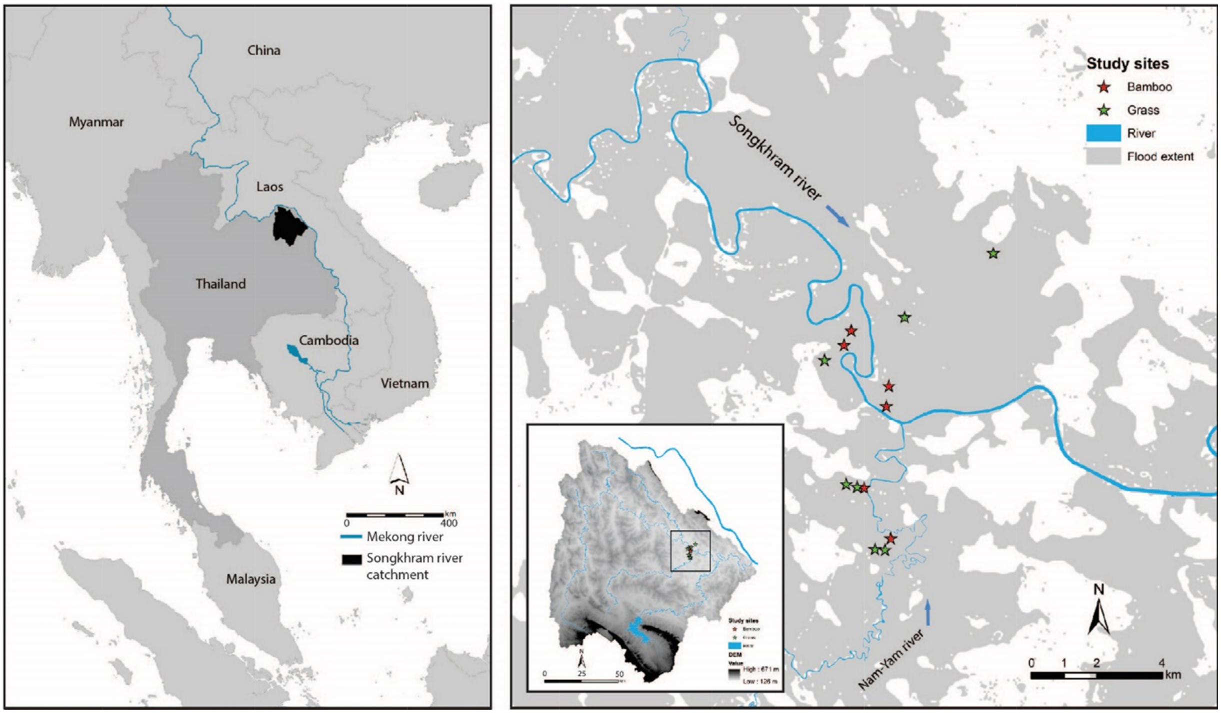

Fig. 1. Location of study area in the lower basin of the Songkhram river where the Nam-Yam tributary joins the main river.

Fig. 2. Dense bamboo thicket close to the river (left) and the grass zone behind the bamboo (right).

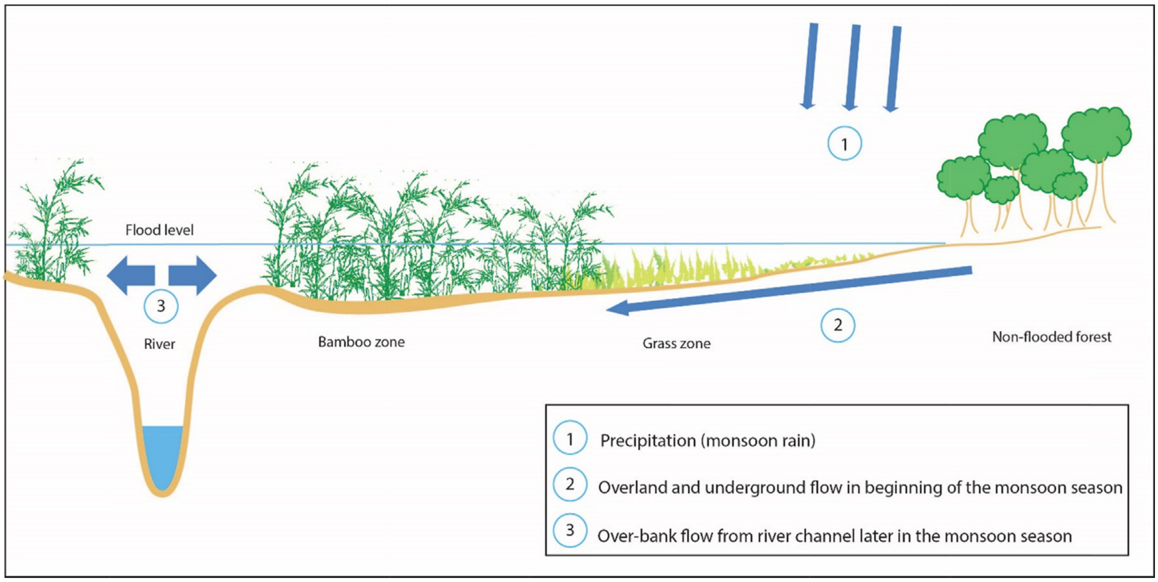

Fig. 3. Conceptual cross-section of the Songkhram monsoon river floodplain, showing characteristic vegetation zonation and hydrological system. At the start of the monsoon season: (1) rainfall is intense and (2) overland and underground flow of water and transport of dissolved solids from the floodplain increase overland. During this period, bamboo and grass grow rapidly until the river overflows (3) and the floodplain enters the aquatic phase.

river bank and extended over the vegetation gradient of the bamboo thicket on the river bank and the grass communities behind (both of which are inundated during the monsoon), as far as the higher-lying non-flooded forest zone (see Figs. 2 and 3). Vegetation, soil, and floodwater were sampled during different periods in 2015: Fig. 4 depicts them in relation to rainfall and river water levels.

3.2. Vegetation sampling and analysis

The bamboo fresh mature leaves were sampled in February 2015 in order to determine nutrient concentrations (see below): we took samples from 15 different locations distributed over the seasonally flooded bamboo zone. Aboveground standing crop was harvested as a proxy for annual plant production. As the bamboo produces fresh shoots and leaves all year round, we counted the newly formed shoots per m^2 and ignored the shoots from previous years. Shoots were dried and weighed in order to estimate the aboveground annual production (g dry wt/m^2).

For the grass zone, we harvested aboveground living biomass from 9 locations in August 2015, which was when grass growth had peaked following monsoon rain water input. At each location, three 50×50 cm plots were harvested. The bamboo leaves and the grass biomass were dried at 105 °C for 4 h and the standing crop was expressed as g dry wt/m^2. The three replicates were averaged.

The dry plant material was ground and analyzed for nitrogen (N) and carbon (C) using a C/N analyzer. Part of the ground sample was digested by nitric acid (65% HNO_3) and analyzed for phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), zinc (Zn), aluminum (Al), silica (Si), iron (Fe), sulfur (S), and manganese (Mn) using Inductively Coupled Plasma Optical Emission Spectrometry (ICP-OES).

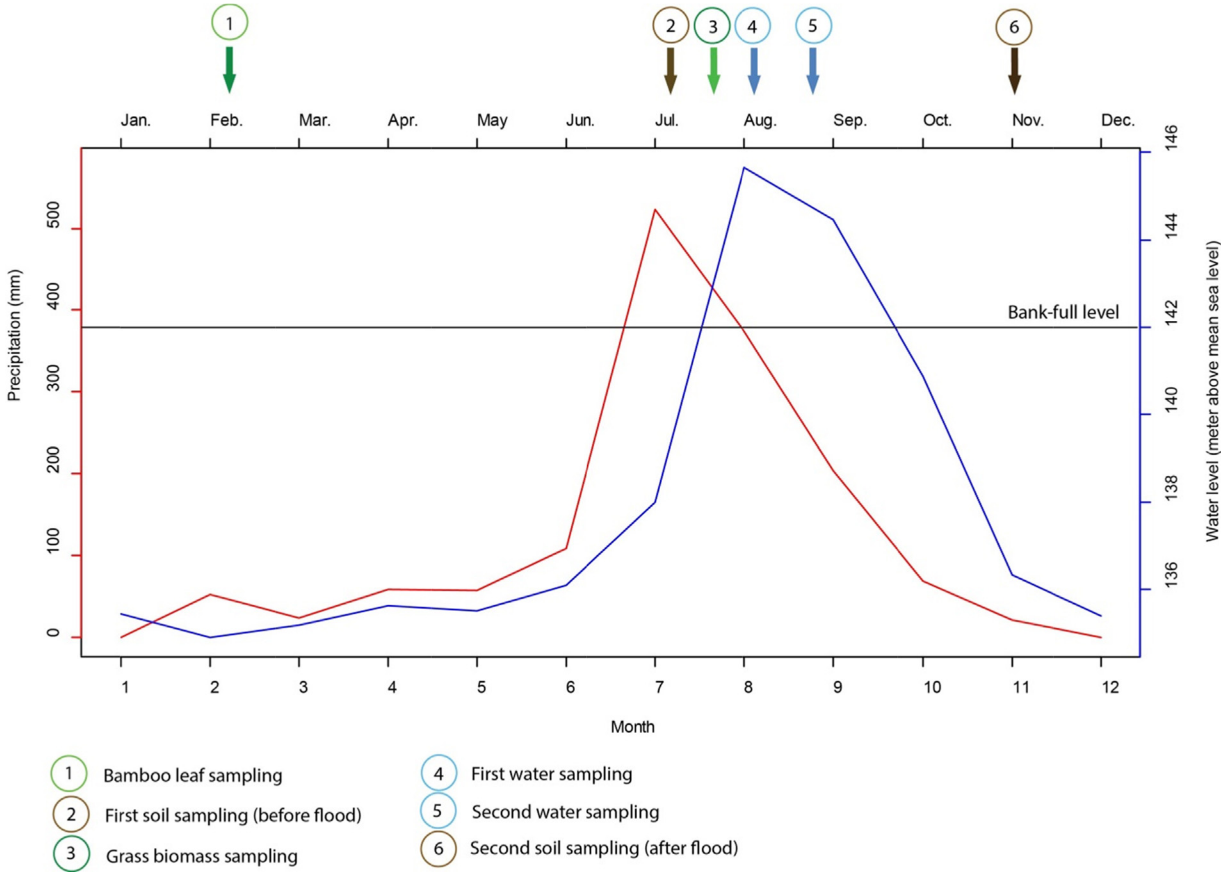

Fig. 4. Rainfall (red line) and water level (blue line) of the Songkhram river in 2015, with indication of sampling moments of soil, water, and vegetation.

3.3. Soil sampling and analysis

Soil samples were collected during two field campaigns – before the flood (June–July 2015) and after the flood (November 2015) – at the same locations. Seven of the sites were in the bamboo zone and 6 were in the grassland zone. The soil samples were taken using a stainless steel soil corer (5.2 cm long, 5 cm diameter). Three cores were collected at each site (in an area of ca.10 m^2).

Soil samples were air dried at room temperature for 2 weeks. After drying, the soil was ground and sieved through a 0.5 mm sieve for further chemical analysis. Soil pH was measured from a solution of 10 g soil sample with 10 ml of demineralized water. The available phosphorus (P) in the soil sample was determined from 5 g of soil, using Bray 2 solution as extractant. The concentration of the extractable phosphorus was determined by colorimetric and spectrophotometric methods. Ammonium exchangeable potassium (K) in the soil sample was also determined from 5 g of soil, using 1 M ammonium acetate as extractant. The K concentration in the extracted solution was determined using a flame photometer. Total organic carbon (TOC) and total nitrogen (TN) were determined by the Walkley–Black and macro Kjeldahl digestion methods, respectively.

3.4. Floodwater sampling and analysis

In total, 33 samples of floodwater were collected at two stages of the flood. The first (17 samples) was obtained during the peak flood (10–15 August 2015), the second (16 samples) was obtained while the flood was subsiding (27–28 August 2015). Along each transect the sampling sites were in the main river channel, in the bamboo zone, and in the grass zone.

At each site, 4 l of water were collected from approximately 30 cm below the level of the floodwater, using a polyethylene (PE) bottle which was pre-washed by the water to be sampling onsite. To collect a sample, the bottle was dipped into the floodwater. As soon as a sample had been taken, its EC, temperature, dissolved oxygen, and pH were determined. The sample was then stored in a cooler at approximately 4 °C. The depth of floodwater at each site was measured using a measuring tape weighted at one end.

The water samples were delivered to a laboratory for preparation and treatment within 24 h of collection. Each sample was mixed thoroughly and then divided into three subsamples. The first subsample was filtered through 0.45 μm cellulose acetate membrane filter and divided into two aliquots of 50 ml. To the first, 1 ml of nitric acid

(65% concentration) was added, for ion analysis by means of ICP-OES. The second was not acidified and prepared to analyze dissolved organic carbon (DOC) and total dissolved nitrogen (TDN).

The second subsample was prepared for unfiltered water analysis. Aliquots of 250 and 125 ml from this unfiltered subsample were stored in wide-mouth PE bottles. The first 250 ml was acidified by adding 2 ml of 65% concentrated nitric acid for total phosphorus (TP) analysis. The 125 ml was not acidified prior to analyses for TOC and total nitrogen (TN). Prior to analysis, all samples were kept in cool (ca. 4 °C) and dark conditions. Additionally, within 24 h of collection, a 5 ml aliquot was taken and its alkalinity was measured using a HI-3811-100 chemical test kit (Hanna Instruments, 2016).

The third subsample was prepared to determine total suspended solid (TSS) and organic matter (OM). Between 500 and 1000 ml (depending on filtration speed) was filtered through 0.7 μm Whatman GF/F glass fiber filter of known weight. The filter with its residual suspended solid was then dried at 105 °C for 24 h, cooled in a desiccator and weighed. Subsequently, the filter was combusted at 400 °C for 16 h and the weight after combustion was used to determine the amount of OM lost during combustion.

3.5. Determination of nutrient limitation in vegetation

To determine the type of nutrient limitation we followed Venterink et al. (2003), who used a method based on critical values of N:P, N:K, and K:P ratios in aboveground plant material. N-limited sites were those with N:P ratio <14.5 and N:K ratio <2.1, whereas P-limited sites and sites limited in both P and N were those with a N:P ratios >14.5 and K:P ratios >3.4. Sites limited in K or in K + N were those with N:K ratios >2.1 and K:P ratios <3.4.

3.6. Estimation of nutrient storage in soil and vegetation and input from floodwater and atmosphere

The total N and available P and K in the soil were determined by analyzing the top 5 cm of each soil core. Concentrations of total N, and available P and K in mg per gram soil were multiplied by the soil bulk density (g soil per m^3 volume) and the volume of the top 5 cm soil in 1 m^2.

To obtain an indication of the annual aboveground nutrient storage (g nutrient/m^2) in the bamboo zone we multiplied the dry weight/m^2 by the nutrient (N, P, and K) concentrations measured in the fresh leaves (mg nutrient/g dry wt), assuming this to be a reasonable estimate for the whole shoot. For the grass zone, we used the sampled aboveground biomass of grass (g/m^2) and multiplied it by the nutrient concentrations (mg nutrient/g dry wt) in the grass biomass sample of each site.

To estimate the potential amount of nutrients imported by floodwater to a certain area we averaged the concentrations of nutrients and the depth of floodwater for the 2 flood stage from each site. The volume of standing water (l/m^2) was calculated from the average depth of each site. Then the average nutrient concentration was multiplied by the volume of the standing water (l/m^2). By using the above method, we assumed that the system works with a peak discharge in the floodplains after which no new water enters the floodplain anymore, and only water outflow takes place after the peak. If this is the case it is justified to use our calculation. An alternative would be to consider every time step a new inflow, and probably also outflow, but we did not observe any indication for this in the field.

Total N and K from atmospheric deposition in Thailand was extracted from World Data Centre for Precipitation Chemistry (Vet et al., 2014).

4. Results

We found significant differences between the bamboo and grass zones (Table 1). Both before and after the flood, the soil in the bamboo zone had significantly higher OM contents, higher total N and K contents, and lower bulk density. Before the flood, the soil in the bamboo zone had higher organic carbon (TOC) and available phosphorus (P), and lower C/N ratio than the grass zone. These results indicate that the bamboo soil is more fertile than the grass soil. However, the high C/N ratios in both zones (bamboo ≥52, grass ≥48; Table 1) indicate that both soils have poor N fertility. After the floods, a significant decrease of organic carbon from the soil in both zones is found and further the drop in the C/N ratio shows that the floods export organic carbon from the floodplain and fertilize both zones.

Comparison of the water samples taken at the peak of the flood and during its recession reveals that after the peak, sedimentation of suspended matter occurs and the concentration of dissolved solid increased, possibly due to

Table 1
Soil characteristics and soil nutrient concentrations before and after flooding for the bamboo and grass zones: comparison of means (±standard error of the mean). Values with different letters (a, b and c) indicate significant differences ($p < 0.05$; paired t-test for within zone and independent t-test for between zone).

Variable (soil)	Bamboo (n samples = 21)			Grass (n samples = 18)		
	Before flood	After flood	% change	Before flood	After flood	% change
pH	4.41 ± 0.04 a	4.73 ± 0.03 b	7	4.46 ± 0.03 a	4.86 ± 0.04 c	9*
Bulk density (g/cm^3)	0.27 ± 0.01 a	0.26 ± 0.01 a	−4	0.33 ± 0.01 b	0.34 ± 0.01 b	3
Organic matter (g/kg)	56.6 ± 3.7 a	54.9 ± 3.5 a	−3	27.0 ± 2.3 b	25.7 ± 2.5 b	−5
Organic carbon (g/kg)	118.7 ± 10.7 a	88.0 ± 18.1 bc	−26*	86.2 ± 8.1 b	48.5 ± 8.2 c	−44*
Total N (g/kg)	1.67 ± 0.11 a	1.75 ± 0.11 a	4	0.91 ± 0.08 b	0.95 ± 0.09 b	3
Available P (mg/kg)	11.9 ± 1.1 a	8.8 ± 1.8 bc	−26*	8.6 ± 0.8 b	4.9 ± 0.8 c	−44*
K (mg/kg)	127.0 ± 12.8 a	114.3 ± 10.0 a	−10	70.8 ± 7.5 b	48.0 ± 5.8 c	−32*
C/N ratio	74 ± 6 a	52 ± 9 b	−30*	95 ± 19 c	48 ± 5 b	−49*

* Indicates variable changed significantly after flooding ($p < 0.05$; paired t-test).

Table 2
Floodwater chemistry from Songkhram river floodplain: comparison of the mean (±standard error of the mean (SE)) nutrient concentration from the first sampling during flood peak periods and the second sampling sample during subsidence of the flood (two weeks after the first sampling). Asterisked values indicate a variable with significant difference ($^{*}p < 0.05$, $^{**}p < 0.01$, paired t-test). NA indicates values below the method's detection threshold.

Variables (water)	Units	Mean ± SE		% change
		First sampling (n samples = 17)	Second sampling (n samples = 16)	
Temperature	°C	32.2 ± 0.3	33.3 ± 0.3	3*
Depth	meter	4.1 ± 0.1	1.6 ± 0.3	−61**
EC	µS/cm	41.3 ± 2.3	88.4 ± 9.4	114*
DO	mg/l	4.8 ± 0.4	1.9 ± 0.2	−60**
pH	–	6.8 ± 0.04	6.5 ± 0.02	−4**
Alkalinity	mg/l	17 ± 0.7	20 ± 0.7	18**
TSS	mg/l	4.72 ± 0.26	2.60 ± 0.29	−45**
OM	mg/l	1.30 ± 0.06	1.34 ± 0.08	3
TOC	mg/l	4.35 ± 0.12	5.00 ± 0.17	15**
DOC	mg/l	3.62 ± 0.10	4.80 ± 0.08	33**
TN	mg/l	0.68 ± 0.03	0.64 ± 0.03	−6
TDN	mg/l	0.50 ± 0.02	0.53 ± 0.01	6*
TP	mg/l	0.05 ± 0.01	0.04 ± 0	−20*
PO_4^{3-}	mg/l	0.04 ± 0	NA	NA
K^{+}	mg/l	1.64 ± 0.02	2.38 ± 0.15	45**
Mg^{2+}	mg/l	0.73 ± 0.03	1.24 ± 0.05	70**
Mn^{2+}	mg/l	0.02 ± 0	0.06 ± 0.01	200**
Ca^{2+}	mg/l	2.12 ± 0.1	3.63 ± 0.17	71**
Cl^{-}	mg/l	13.59 ± 1.64	24.67 ± 3.46	82**
$Fe^{2+/3+}$	mg/l	0.29 ± 0.02	0.53 ± 0.03	83**
Na^{+}	mg/l	6.67 ± 0.52	15.07 ± 1.74	126**
S^{-}	mg/l	0.59 ± 0.08	0.61 ± 0.03	3
Si^{+}	mg/l	1.50 ± 0.04	1.89 ± 0.07	26**

high evapotranspiration caused by the high tropical temperatures (30+ °C) (Table 2). This is reflected in decreases in TSS and increases in EC, Cl, and other major ions. During the subsidence of the flood, dissolved oxygen (DO), TP, and PO_4^{3-} also decreased significantly in the floodwater and alkalinity increased (Table 2), probably because of the algal blooms we observed during the second sampling.

The productivity of the bamboo vegetation is high: estimated to be ca. 5 ton dry wt/ha/yr of aboveground biomass. The grass zone is also productive, though less so: it averaged >3.5 ton dry wt/ha/yr (Table 3). Analysis of aboveground plant tissue indicates that concentrations of all three major nutrients (N, P, and K) are significantly higher in the bamboo vegetation zone than in the grass zone. Nutrient ratios indicate that bamboo growth is limited by P (or co-limited by P and N) whereas the vegetation of the grass zone is limited by N. We did not find any indications of K co-limitation (Table 3).

Table 3
Comparison of mean and standard error (SE) of the vegetation tissue nutrient constituents of bamboo leaves and grass aboveground biomass (units in mg element per g of biomass dry weight).

Variables (Plant)	Unit	Mean ± SE	
		Bamboo (n samples = 15)	Grass (n samples = 27)
C	mg/g-dry wt	408.7 ± 4.5	425.2 ± 2.6
N	mg/g-dry wt	18.7 ± 0.8*	6.31 ± 0.30
P	mg/g-dry wt	1.26 ± 0.08*	0.68 ± 0.05
K	mg/g-dry wt	10.5 ± 0.5*	7.45 ± 0.30
Al	mg/g-dry wt	0.64 ± 0.04*	0.37 ± 0.04
Ca	mg/g-dry wt	4.32 ± 0.25*	1.60 ± 0.09
Fe	mg/g-dry wt	0.41 ± 0.02*	0.25 ± 0.03
Mg	mg/g-dry wt	1.11 ± 0.07	0.97 ± 0.05
Mn	mg/g-dry wt	0.42 ± 0.04*	0.25 ± 0.02
S	mg/g-dry wt	2.03 ± 0.09*	1.06 ± 0.04
Si	mg/g-dry wt	1.25 ± 0.04*	0.97 ± 0.04
C/N	–	22.2 ± 0.9	70.4 ± 2.6*
C/P	–	340 ± 19	726 ± 61*
N/P	–	15.4 ± 0.7*	10.7 ± 1.0
K/P	–	8.5 ± 0.4	12.6 ± 1.1*
N/K	–	1. 83 ± 0.09*	0.91 ± 0.08
C/K	–	40.4 ± 2.3	60.1 ± 3.2*
Above-ground production	g/m^2	521 ± ? (n = 1)	386 ± 58 (n = 6)

* Indicates variable that is significantly higher (independent t-test, $p < 0.05$).

5. Discussion

5.1. Similarities and differences in ecological functioning between temperate and tropical floodplains

Integration of our data on soil, water, and vegetation led to the emergence of a coherent pattern of flood-related nutrient and carbon fluxes that are spatially and temporarily differentiated. First, the significant loss of organic carbon from the soil after the flood indicates that the floodplain is a source of carbon and this carbon is probably exported downstream. This is also illustrated by the DOC and TOC in the floodwater, which increase significantly after the floodplain becomes an aquatic system while inundated. This implies that organic carbon produced in the floodplain is exported via the retreating floodwater. This was also reported by Zuijdgeest et al. (2015) for the floodplain along the Zambezi in Southern Africa, where OM that had been produced upstream was transported downstream and was exported. This illustrates how large floodplain systems act as large biogeochemical reactors that behave distinctly different from the rest of the catchment (Zuijdgeest et al., 2015). In our case, the part of the floodplain we sampled seems to be a source of carbon for the river and downstream areas.

Second, we clearly observed a role of the vegetation zonation in floodplain functioning. In the Songkhram floodplain, clear zonations of bamboo and grass are present. It was found earlier that for tropical floodplains vegetation patterns in structure and community are determined by the duration and the depth of the flood (Arias et al., 2016; Parolin et al., 2016). In addition to these main factors, the hydrochemistry of inundated water, and the soil and topography can cause stress in vegetation functioning and therefore cause patterns in vegetation. In the tropics, where vegetation production is optimal around the year, adaptation to flood stress seems to be the key mechanism of spatial heterogeneity in species community (Parolin and Wittmann, 2010). Further Arias et al. (2013) showed that the mean annual flood duration and soil properties determined canopy height, canopy cover and above ground biomass of the Tonle Sap floodplain forest in Cambodia. In our Songkhram river floodplain the zones of bamboo and grass experience different stresses, 1) a higher flood stress, higher nutrient input, and higher productivity in the bamboo zone and 2) a lower flood stress, lower nutrient input, and lower productivity in the grassland.

The bamboo experiences higher flood depth and duration which force the bamboo to quickly take up available nutrients and having fast shoot growth to escape from the flooding. The higher productivity is supported by additional nutrient uptake from the flood water. As a result, OM production is much higher in the bamboo zone than in the grassland, leading to higher OM content in the soil of the bamboo zone. This difference is attributable not only to the vigorous growth of the bamboo but also, at least partly, to the prominent algal blooms in this zone. After the floods have receded, these algae remain on the ground and start to decompose rapidly in the warm and still moist conditions. Comparison of the temperatures in our tropical catchment with the temperature ranges of seven large floodplains in North America and Europe reported in Spink et al. (1998) shows that the temperatures in Songkhram are very different: they are consistently very high.

The grassland zone is usually found next to the bamboo zone. Although the flood depth and duration in this zone is lower than the bamboo zone due to its topography, vegetation in this zone is fully submerged. Limited nutrients in this zone leads to a lower productivity. Therefore the combination of flood stress and nutrient limitation determines the vegetation in this zone.

Interestingly, we found the Songkhram is very similar to the river Shannon in Ireland in terms of catchment size, discharge, and soil and vegetation nutrient contents (data on the Shannon reported by Spink et al., 1998). The Shannon is a typical example of a predominantly rainwater-fed river poor in solutes, as is the case for the Songkhram river, and also for the Siberian river Ob, which is fed mainly by snow melt (Schipper et al., 2007). In the floodplains of these three rivers with very different climates, vegetation production is driven more by sedimentation and mineralization of OM than by dissolved nutrients brought in by floodwater.

Although the Songkhram floodwater exports OM from the floodplain, it is also evident that the floods import sediment and nutrients. The water samples taken and flooding depths measured at the peak and at the end of the flood period illustrate this. At the peak of the flood the floodwater is very deep: on average 4 m; after the monsoon rains had ceased, the concentration of TSS in the sampled water was only half of the peak flood's TSS concentration (Table 2). Visual observations also revealed that the water at the second sampling was much more transparent.

5.2. Nutrient budgets

We roughly estimated the nutrient budgets for the bamboo and the grass zone (see Section 3.6) and were able to further differentiate between N, P, and K fluxes and reserves (Fig. 5), although it must be noted that our estimates are only rough, approximating indicators.

Nitrogen: Although atmospheric deposition of N in the Songkhram catchment is significant (6.5 kg N/ha/yr) it is moderate compared to the deposition in other areas in S.E. Asia (Vet et al., 2014) and the floods bring in twice as much N into the grass zone and three times as much into the bamboo zone than is deposited from the atmosphere (Fig. 5a). Most of the N stored annually in the aboveground biomass must thus be obtained from the soil. This is especially evident for the bamboo zone, since the N from atmospheric N deposition plus the estimated N input via the flood add up to far less than the N in biomass. Additional N input to the system can also relate to large particulate organic matter (POM) from flood water. N from the floodwater is rather not (only) originating from dissolved organic matter, but also relates to POM. This POM in flood water would also be an important source for N input to the floodplains. This is also demonstrated by our data, showing that water OM did not change but TOC and DOC increased in the second sampling. This indicates that organic matter is also a source for nutrients during the flood. N from the POM is then filtered by the bamboo, deposited on the soil and becomes quickly part of the soil through bioturbation (Mermillod-Blondin, 2011).

Our schematic cross-section in Fig. 5 also reveals that the bamboo zone may function as a filter, trapping most of the N from the floodwater before the water reaches the grass zone further away from the river.

Phosphorus: Atmospheric deposition of P is probably negligible, unless dust storms occur, which to our knowledge has not been the case. It appears that compared with the amount of P that could hypothetically be imported from the atmosphere and the floods, the amount of P stored annually in aboveground biomass is four times higher in the bamboo zone and two to three times higher in the grass zone. So, as was the case for N, the soil must also be an important source of P. Remarkably, the soil in both zones contains only minor amounts of P, which implies that most of the available P is taken up rapidly, as is also observed in tropical forests, where almost all nutrients are

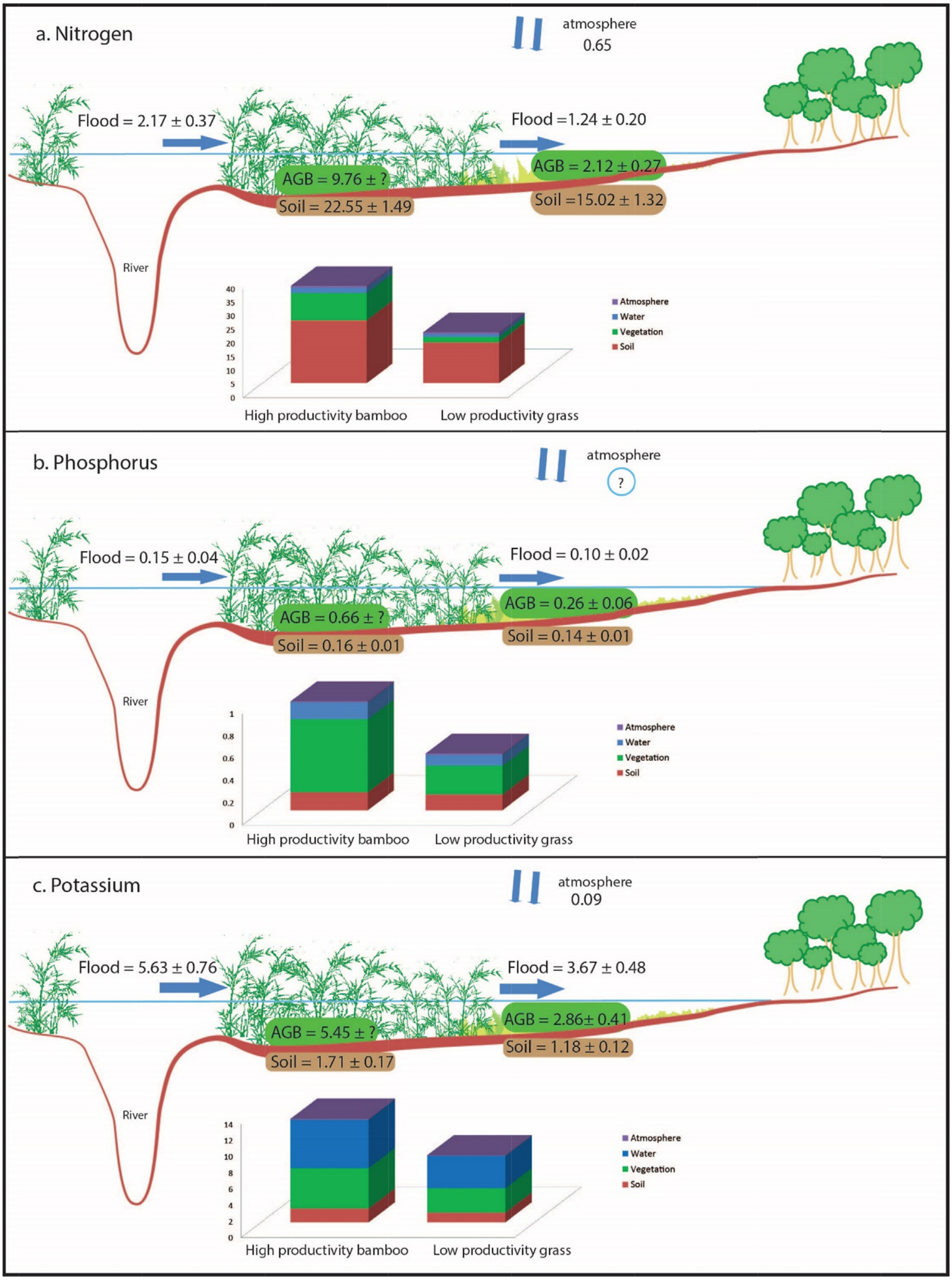

Fig. 5. Estimated N, P, and K storage in soil and vegetation and the contribution of floodwater and atmospheric deposition. The numbers represent Mean ± SE (g/m^2).

sequestered in standing vegetation (Vitousek and Sanford, 1986). The bamboo zone may – as was the case for N – also filter out P, taking up P from the floodwater before it reaches the grass zone further away from the river.

Potassium: It is very clear that the flood is the major source. Compared to the amount of K available in the soil and the amount of K deposited from the atmosphere, the potential input of K from the floods is important. Again, we speculate that the bamboo zone may function as a filter, taking up K from the floodwater before it reaches the grass zone more distant from the river. As illustrated in Fig. 3, which shows (i) some depression within the bamboo zone, and (ii) the bamboo zone to be wider than the grass zone in the higher 'flooding littoral' it should not be surprising that the bamboo is the dominant filtering vegetation unit, especially regarding the height above the mean and the bank full water levels.

Comparison of our very roughly estimated nutrient flows with the flows reported by other studies in river floodplains reveals some general patterns. Our findings are similar to those of Venterink et al. (2002) for temperate European river systems. These authors also found most of the N in aboveground vegetation was obtained from turnover in the soil, but they also concluded that the input of P and K from the river must have been substantial. In another study performed in the floodplain of the European river Rhine, Venterink et al. (2006) reported similar findings to ours: sediment deposition was an important mechanism of retention of nutrients, especially of P, and nutrient retention was much greater in reed-beds – comparable to our bamboo zone – than in grasslands. The authors postulated that the high sediment deposition rate in their floodplain reed-bed was the result of the roughness of the vegetation structure, which reduced the water velocity, facilitating sedimentation and trapping nutrients. In contrast to this, McJannet et al. (2012) argue that in tropical riverine wetlands where there is strong seasonality in flows and short residence time during the periods of maximum sediment and nutrient loads, there is likely to be limited overall filtering potential. This aspect certainly needs further study, although our results support the hypothesis we put forward in our previous study (Walalite et al., 2016), that the high annual biomass production of the bamboo zone is driven by the floods which import nutrients and sediments filtered out by this zone. The less productive grassland zone located behind the bamboo receives less input of nutrients from the river.

If we focus on the type of nutrient limitation we notice that, in contrast to what we found for Songkhram, Venterink et al. (2006) found low N:P ratios in their reed vegetation along the river Rhine, indicating N limitation; our bamboo zone is clearly P-limited, as can be inferred from the N:P ratios we found. Comparison of our data with the data from the floodplain of the river Biebrza in Poland (Venterink et al., 2009) reveals that in the Biebrza floodplain vegetation both N and P are lower, whereas K is slightly higher. Nevertheless, there are also indications for the Biebrza floodplain to be P-limited, as is our bamboo zone. When Spink et al. (1998) experimentally tested nutrient limitation by conducting fertilization experiments in seven floodplains, they found that only in one floodplain – the Irish river Shannon – plant growth was nutrient-limited (in their case, N- and P co-limitation). In the other six floodplains, climatic factors (temperature, latitude) seemed to be the dominant drivers of productivity. Thus it seems that most river floodplains do not face nutrient limitation. In cases where nutrient limitation has been found, both the monsoon river Songkhram and the temperate rivers Biebrza and Shannon differ from the river Rhine in that their vegetation is limited or co-limited by P. The absence of P limitation in the Rhine floodplain is probably attributable to the large input of P by the river Rhine, the water of which contains wastewater discharge and runoff from farmland in the human-dominated catchment of the Rhine (Billen et al., 2011). This has also been observed in other human-impacted rivers in Europe and North America (Caraco and Cole, 1999; Sjodin et al., 1997). Perakis and Hedin (2002) sampled rivers from 100 unpolluted primary forests in temperate South America and compared them to streams in polluted regions in temperate North America, concluding that in unpolluted regions the stream water nitrate concentrations were low and dissolved organic nitrogen was responsible for most of the nitrogen losses from these forests. It is, however, unclear if this also holds for tropical rivers in unpolluted areas. Putting the scarce information about N and P cycling and fluxes in tropical rivers and the role floodplains play into perspective, it is clear that we are only beginning to understand how N and P cycling is driven by climate, river characteristics, and human interference, and how important floodplain processes are in nutrient cycling and retention.

Conflict of interest

None declared.

Ethical statement

Authors state that the research was conducted according to ethical standards.

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