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Floodplain plant productivity is better predicted by particulate nutrients than by dissolved nutrients in floodwater

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ABSTRACT

When rivers flood, nutrients exchange between the river and the floodplain, enhancing floodplain vegetation productivity, as described by the flood pulse concept. However, river water may not reach the edge of the floodplain if there are other sources of inundation water. Also, particulate nutrients travel less far from the river than dissolved nutrients and are more likely to remain available to vegetation during the growing season. This would mean that high nutrient input by river water, and associated high floodplain plant productivity, likely occurs only in the vicinity of the river channel. This paper tests 3 hypotheses derived from these observations related to the validity of the Flood Pulse concept and the relation between floodplain plant productivity and dissolved resp. particulate nutrients.

We mapped particulate nutrient and dissolved nutrient concentrations in floodplain inundation water across the Biebrza floodplain (Poland), and assessed their spatial relationships with topographical parameters, aboveground biomass and species richness. Particulate nitrogen (N) and phosphorus (P) deposition and dissolved N decreased significantly with distance from the river and with elevation, and increased significantly with water depth. Dissolved P was not significantly correlated with topographical parameters or water depth. Aboveground biomass correlated significantly with particulate N and P deposition, but not with dissolved N or P.

We conclude the edge of inundation is a poor predictor of the zone of high productivity. Nutrient input is higher near the river channel due to deposition of particulate nutrients, which are thus more relevant for vegetation productivity than dissolved nutrients. Spatial particulate nutrient patterns should therefore be integrated in monitoring programmes for policy and research. We further recommend refining the flood pulse concept to take into account the spatial deposition of river derived particulate nutrients, as well as non river-derived inundation water sources.

1. Introduction

Located at the interface of water and land, floodplains are among the most productive and diverse ecosystems (Ward et al., 1999). They host high biodiversity because of dynamic environmental processes and gradients of e.g. nutrient availability and saturation (Ward et al., 2002). Agriculture and fisheries depend on floodplains being very fertile systems because of their periodic inundation with river water rich in sediment and nutrients (Auerbach et al., 2014; Barbier, 1993; Welcomme, 2008). In many parts of the world, however, floodplains are at risk, with disturbance to the natural hydrology (Bunn and Arthington, 2002), land use change (Syvitski et al., 2009) and deterioration of water quality and eutrophication (Smith et al., 2006) being major threats for floodplain functions and biodiversity (Bouwman et al., 2013; Brinson and Malvárez, 2002).

To curb current and future deterioration of floodplain ecosystem services, there is a need to understand and quantify the possible effects of these processes on the hydrological cycle and biogeochemical processes in floodplains. The main drivers of floodplain ecosystem services can be conceptualised as a cause-effect chain determining vegetation characteristics, with large-scale spatio-temporal environmental conditions steering progressively lower-scale site conditions in a geohydrological setting (De Mars, 1996). On the floodplain, topographical differences and geomorphology affect the spatially explicit hydrological flow processes of river flooding, precipitation accumulation and groundwater discharge. Hydrology is therefore the principal driver of

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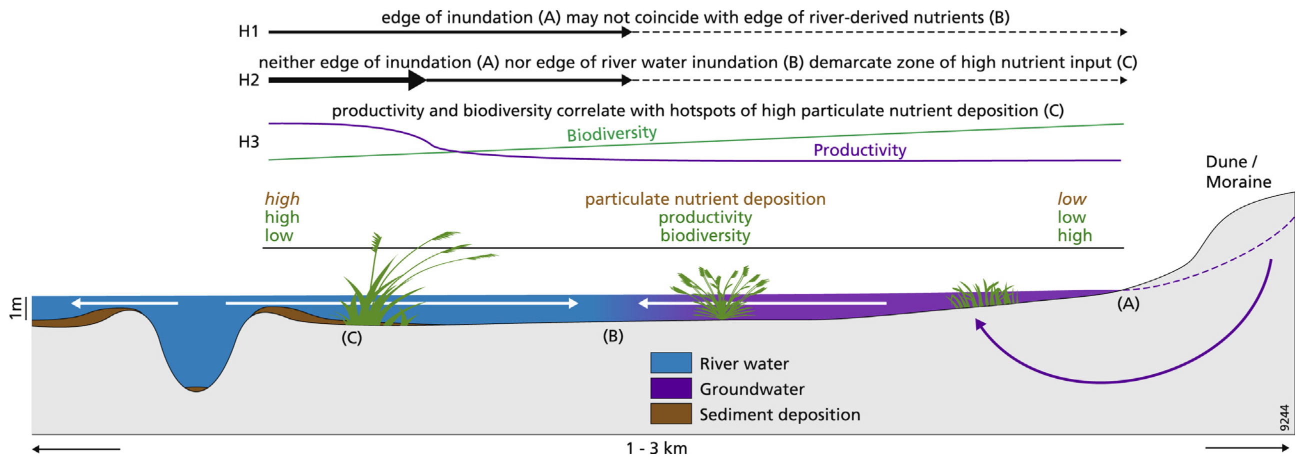

Fig. 1. Cross section depicting Biebrza floodplain inundation water types (river flooding, groundwater discharge, mixing) in relation to particulate nutrient deposition, vegetation productivity and biodiversity. Hypotheses are indicated above the cross-section.

spatio-temporal patterns in water availability, transport of major ions and nutrients, biogeochemical soil processes and nutrient availability (McClain et al., 2003), and, ultimately, ecosystem productivity, structure and biodiversity (De Mars, 1996).

One of the major hydrological processes affecting floodplain ecosystems is flooding with river water. This lateral exchange between the river and floodplain was first conceptualised by the holistic flood pulse concept (Junk et al., 1989), which attributes floodplain nutrient status to input of sediment and nutrients from the river during flood pulses, and by decomposition and mineralisation during dry phases. The flood pulse concept focuses on the moving edge of inundation (the 'moving littoral'), which causes wetting and drying, ultimately steering productivity. The flood pulse concept was originally derived for tropical Amazonian floodplains, South-East Asian rivers and the Upper Mississippi River (Junk et al., 1989), where river flooding is the main driver of floodplain inundation. However, there are two fundamental aspects for which the flood pulse concept needs reconsideration, particularly in relation to temperate rivers.

First, several studies on river flooding have shown that floodplain inundation water is not necessarily derived solely from the river. Sediment-loaded Amazon river water and sediment-free backwaters could be clearly distinguished on remote sensing images (Mertes et al., 1997). Rudorff et al. (2014) showed seasonally varying influence of river water, direct rain, runoff and groundwater seepage in an Amazon floodplain. For 13 small Dutch floodplains, Beumer et al. (2008) found that the river flood pulse blocked drainage of precipitation, snowmelt, or exfiltrating groundwater. For the Lower Biebrza Basin (Poland) inundation water has been shown to derive from groundwater discharge and snowmelt over significant stretches of the floodplain (Chormański et al., 2011; Keizer et al., 2014). Other than these studies, research on water quality patterns in floodplain inundation water has been scarce, which is surprising, as this might elucidate the ecohydrological functioning of river floodplains (Keizer et al., 2016).

A second shortcoming of the flood pulse concept is that, although it describes the two forms of nutrients: dissolved and particulate, i.e. attached to sediment and as organic matter and detritus (Worsfold et al., 2008), it does not take into account spatial variation in input. Particulate nutrients may comprise a significant part of the P loads and, to a lesser degree, N loads. In inundation water of the Everglades wetlands, between 20–43% of total P and 2–11% of total N was found to be transported in particulate form (Noe et al., 2007). Comparable fractions were reported for rivers in the UK (25–75% for P, 3–8% for N; Walling et al., 1997), and the river IJssel in the Netherlands (50–70% for P, 2–3% for N; Olde Venterink et al., 2003). Russell et al. (1998) assessed dissolved and particulate N and P fractions in two Welsh rivers and found 26–75% of total P and 3–8% of total N was transported in particulate form.

It seems likely that during flooding, river-derived particulate nutrients behave fundamentally different from dissolved nutrients. Whereas dissolved nutrients may be transported throughout the river-inundated zone, particulate nutrients will probably not and remain closer to the river channel, since sediment deposition generally decreases with increasing distance from the river due to the decrease in flow velocity (Allan, 2004). Decreasing sedimentation loads with distance from the river have been shown for temperate lowland river floodplains in Denmark, the UK, the Netherlands and Poland (see e.g. Kronvang et al., 2009; Kronvang et al., 1999; Middelkoop and Asselman, 1998; Poulsen et al., 2014; Walling and He, 1998; Wassen and Olde Venterink, 2006). Beumer et al. (2007) reported that in Dutch floodplains subject to river flooding, the P content in the soil (e.g. related to particulate P deposition) was higher than that in floodplains where the source of inundation water was precipitation or groundwater. However, possible correlations with ecological parameters were not investigated.

The spatially different spread of river-derived particulate and dissolved nutrients may have consequences for floodplain plant productivity. Nutrient input is only relevant for productivity when imported nutrients are available to plants. Dissolved nutrients in inundation water mainly contribute to plant growth in three ways. First by infiltration of inundation water to the root zone where they can be taken up by the plants. Significant infiltration of inundation water in flooded river valleys is however likely to be hampered when floodplain soils are already water-saturated (Stelmaszczyk et al., 2015). Second, plants can also take up nutrients via their leaves and adventitious or aerial roots (Nadkarni, 1981). We assume this to be negligible in temperate systems as these types of plants are not abundant here. Third, river-derived dissolved nutrients may become available to plants when taken up by algae which become deposited after the inundation recedes, thereby adding to the deposition of river-derived particulate nutrients.

In terms of the relevance of the flood pulse concept for temperate rivers, the above considerations lead to the following hypotheses (Fig. 1).

H1. The edge of inundation is not the edge of river-derived nutrient input when other types of inundation water are present on the floodplain, e.g. runoff or groundwater seepage near the floodplain edges.

H2. Neither the edge of inundation nor the edge of river water inundation demarcate zones of high nutrient input, because particulate nutrients may comprise a significant part of the nutrient inputs, and are likely to be deposited only relatively close to the river.

H3. High floodplain productivity (and biodiversity) correlates less with the edge of inundation than with hotspots of high river-derived particulate nutrient deposition because nutrient availability is enhanced in zones of high deposition.

The magnitudes of sediment and particulate nutrient deposition in wetlands have been studied both from a hydrological perspective (see e.g. Asselman and Middelkoop, 1998; Noe and Hupp, 2009; Poulsen et al., 2014) and from a nutrient budget perspective (see e.g. Brunet and Astin, 2000; James et al., 2008; Olde Venterink et al., 2006). In 2000 it was noted that only a ‘handful of attempts have been made to quantify sediment deposition in any wetland system’ (Hupp, 2000). Since then, the number has not increased much. Even fewer studies have examined particulate nutrient deposition patterns in relation to ecological variables, despite the well-known importance of particulate nutrient input for the floodplain nutrient budget and hence for floodplain productivity and biodiversity. In recent decades, many authors have proposed merging different scientific disciplines in river science into one, e.g. eco-geomorphology (an amalgam of river ecology, hydrology and fluvial geomorphology) (Dunbar and Acreman, 2001; Thoms and Parsons, 2002; Thorp et al., 2006), in order to improve holistic understanding of system functioning and better predict possible future changes.

The goal of this study was to link ecology and hydrology and to determine spatial patterns in the deposition of particulate N and P and dissolved nutrient concentrations and to relate these to aboveground biomass and species richness in a natural floodplain fen with river floodwater influence and presence of other sources of inundation water.

2. Study area

The study was conducted on the floodplains along the natural Biebrza river (NE Poland; 22°30′–23°60′E, 53°30′–53°75′N; Fig. 2). The floodplain site was selected because of i) absence of large-scale alterations in hydrology and water quality (Wassen, 1995), ii) natural sedimentation patterns (Wassen et al., 2002), iii) presence of near-natural undisturbed wetland vegetation patterns (Pałczynski, 1986), and iv) availability of a large body of data on hydrology, hydrochemistry and vegetation (see e.g. Keizer et al., 2014; Keizer et al., 2016; Wassen et al., 2002). The selected floodplain reach (Lower Basin, 453 km^2, 100–106 m amsl) consists of an ice-marginal valley with a width of 3 km in the north, widening to > 15 km in the south. The floodplain is bordered to the east and west by a sand and gravel moraine plateau (135–160 m amsl) and river dunes are locally present.

Flooding occurs annually after snowmelt, starting between February and April, with flooding depths ranging from 0.10 m at the floodplain edges to more than 1.00 m near the river in local depressions (Chormański et al., 2011; personal observations). The floodplain remains inundated until May–June due to the narrow outflow point and gentle longitudinal and transversal slopes.

The floodplain is composed of natural grasslands, frequently inundated mires and peatlands, whose patterns are known to be related to the presence of multiple hydrological processes with associated water quality: flooding with mineral-rich, nutrient-rich river water (high in pH, NO_3^-, K^+, SO_4^{2-}), discharge of calcium-rich groundwater (high in EC, Ca^{2+}, Mg^{2+}, Na^+, alkalinity), and dilution by water from precipitation and snowmelt (Keizer et al., 2014; Keizer et al., 2016; Wassen et al., 2002). In some locations, the discharging groundwater is polluted (elevated in Cl^-, Na^+, K^+, NO_3^-, NH_4^+) due to agricultural activity

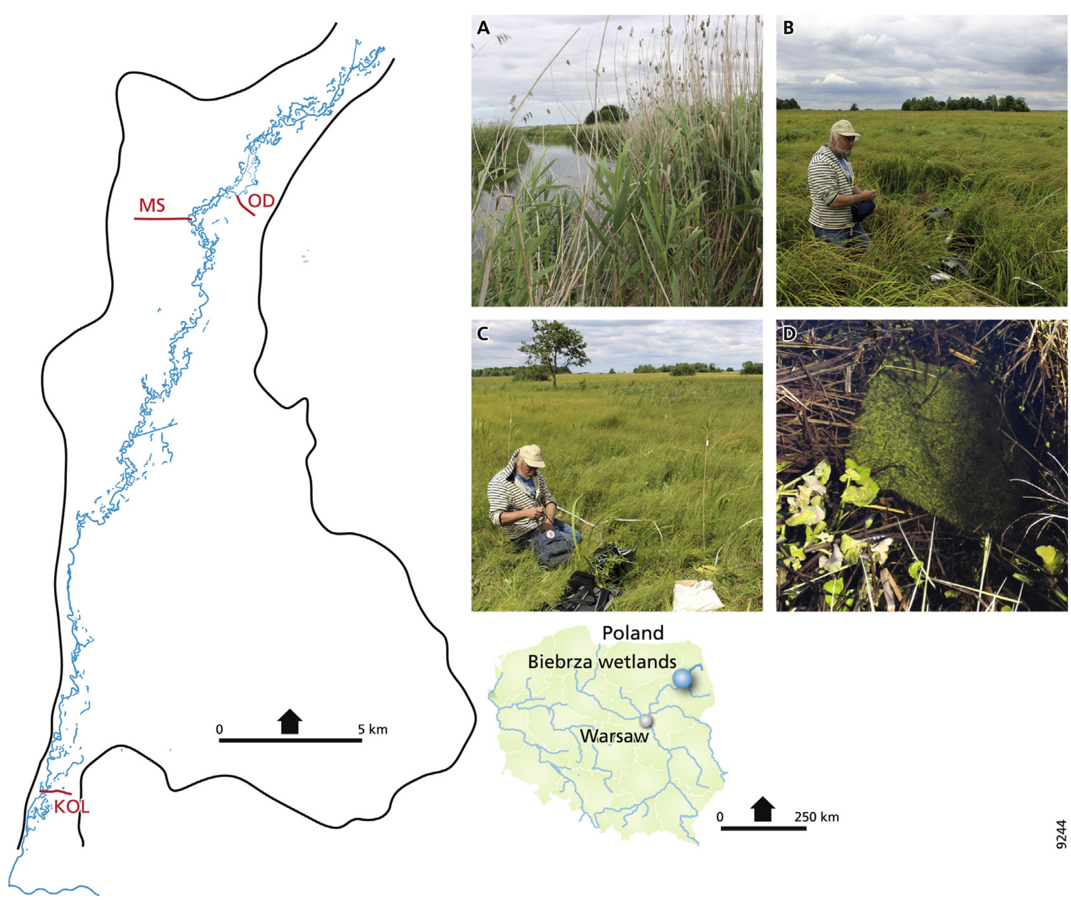

Fig. 2. Location of the Biebrza wetlands (map in centre). The three sampling transects OD, MS and KOL are shown to the left. Examples of typical floodplain vegetation types are shown to the right: A = reeds, B = tall sedges, C = small sedges). D = artificial grass mat (50 × 50 cm) used to trap sediment.

and small settlements upstream (Keizer et al., 2014).

3. Methodology

We formulated 3 hypotheses on processes described in the flood pulse concept with the aim of improving understanding of floodplain processes in temperate rivers with multiple sources of inundation water. To test the hypotheses, we related the spatial patterns of particulate and dissolved nutrient, aboveground biomass and biodiversity to distance from the river, elevation, water depth and the inundation extent of river water, as determined from hydrochemical analysis of the inundation water.

Three transects with 20 sampling points (and 2 duplicates) were installed in October 2014 at representative locations (Fig. 2): two in the northern part on both sides of the river (Olszowa Droga (OD) 7 points: length 850 m and Mscichy (MS) 6 points: length 2050 m) and one in the southern part near the outlet (Kołodzieje (KOL) 7 points: length 850 m). Data was collected between October 2014 and July 2015: deposited particulate nutrients between October 2014 and May/June 2015; elevation, water depth and water quality in April 2015); and aboveground biomass and vascular plant species in July 2015.

3.1. Hydrology and hydrochemistry

Water level and discharge at the upstream ends (Rudzki and Osowiec) and downstream end (Burzyn) of the floodplain was retrieved from the Institute of Meteorology and Water Management – National Research Institute (Poland). Elevation (height above mean sea level) was measured using a differential global positioning system (DGPS) with a real-time kinematic approach (GR-3 TOPCON). In April 2015, the month with highest average flood extent, inundation depths were recorded manually at each sampling point to register the edge of inundation. Elevation above the river water level in October 2014 was calculated for OD and MS transects.

Surface water flow on the floodplain was measured at one-third of the water depth, using an electromagnetic velocity meter designed for low flow velocities (OTT, Nautilus C2000).

To assess the spatial extent of flooding with river water inundation water was sampled (5 cm below the water surface along the transects on 16 April, shortly after peak discharge), and after analysis compared to the characteristics of the main inundation water types in the area as described by Keizer et al. (2014). Because not all points could be reached or were inundated, water samples were taken at 16 of the 20 points. For duplicate points and two sampling points that were close together, only 1 water sample was taken. The water samples were analysed for EC (Electrical Conductivity; $\mu S\,cm^{-1}$, converted to 25 °C measured in the field), pH (measured in the field), alkalinity (at observed pH only as HCO_3^-), Ca^{2+}, Mg^{2+}, Na^+, K^+, Cl^-, SO_4^{2-}, NO_3^-, NH_4^+, PO_4^{3-} (all others in $mg\,l^{-1}$). Dissolved N was calculated as $[NO_3^- + NH_4^+]$-N, dissolved P as PO_4^{3-}-P. Preparation and analysis procedure followed Keizer et al. (2014).

3.2. Particulate nutrient deposition sampling

Particulate nutrient deposition was measured using artificial grass mats of 0.5 × 0.5 m (*cf.* Asselman and Middelkoop, 1998; Steiger et al., 2003) in the 20 sampling points, installed in October 2014 and retrieved in May-June 2015. To analyse local variation in deposition loads and N and P concentrations, the grass mats were installed in duplicate at two locations. Sediment sampling mats had also been deployed in one of the studied transects in 2014, yielding data with which our results could be compared.

After flood recession in May 2015, our sediment mats were collected and stored in plastic bags for three days before transport to the lab. Deposited sediment was rinsed from the mats using deionised water and collected in PE bottles. Well-mixed 50 ml aliquots were taken in quadruplicate in PP tubes and centrifuged at 4000 rpm for 10 min. Excess water was removed and samples were dried for 48 h at 70 °C and weighed for calculation of the sediment load and chemical analysis of the sediment. The sediment was analysed for N, using Fisons NA1500 NCS. The ranges of uncertainty was 0.5–1.0% for N. Total P was determined using an ICP-OES analyser (Spectro Arcos) following total destruction with HF.

3.3. Aboveground biomass and plant species richness

At each sampling location, aboveground living biomass (without bryophytes) was harvested at the end of July 2015 in a 1 × 1 m quadrat, as a proxy for productivity. In some cases, when the vegetation was highly productive and homogeneously distributed, 0.5 × 1.0 m or 0.5 × 0.5 m was harvested. Harvested vegetation was cut, air-dried in the field and within 4 days after collection dried for 72 h at 105 °C and weighed. Vegetation was recorded (cover and abundance of each plant species present) at each sampling location (only once per duplicate) in 3 × 3 m quadrats. As a proxy for biodiversity, vascular plant species richness was taken as the number of unique plant species. Aboveground biomass and species richness was only sampled once per duplicate point. Species richness was not determined for the Kołodzieje transect.

3.4. Analyses

Sediment deposition mats that were not flooded, that were covered in a thick layer of sand, or not found again after the flooding event were removed from the dataset before analysis. The final number of sediment mats used was 18 (including two duplicates). For points that were not flooded, water depths were not used.

First, Spearman's rho correlation coefficients were calculated for dissolved and deposited N and P, aboveground biomass and species richness, and distance from the river, elevation above the river, and water depth at all sampling points.

Second, the edge of river water flooding was identified by comparing floodplain inundation water chemistry during peak flow (16/04/2015) with river water quality during bankfull conditions (samples taken in 2015 on 15/01, 26/02, 31/03 and 16/04). River water quality at the transects was calculated using water quality in the upstream channels of Rudzki Canal and River Biebrza, assuming perfect mixing and that Rudzki contributed 1/3rd and Biebrza 2/3rd to the discharge at the transects. Following Keizer et al. (2014) and Chormański et al. (2011), high pH and high concentrations of NO_3^-, K^+ and SO_4^{2-} in the inundation water indicated influence of river water. Additional evidence of river water flooding was obtained by surface water flow velocity measurements for which it was assumed that measurable flow indicates presence of river water, either as pure river water or a mix with other water types. The spatial distribution of river water in 2015 was compared to inundation water quality patterns of 2001–2012 (Keizer et al., 2014) to compare with observed patterns over longer time periods.

Next, lateral trends in dissolved nutrients and particulate nutrient deposition were compared along the transects in relation to distance from the river, elevation above the river water level in October 2014 and inundation water depth. Lateral trends in aboveground biomass and plant species richness were analysed as functions of: dissolved nutrients in the inundation water; nutrient deposition; distance from the river; water depth in April; and elevation above the river water level in October 2014. We assumed a sediment deposition load above median of all sampling mats to be substantial and to delineate the zone with high particulate nutrient input.

Last, lateral trends in aboveground biomass and species richness were compared to the spatial positions of i) the zone with high particulate nutrient deposition, ii) the zone with river water influence, and iii) the edge of inundation.

All statistics were performed in SPSS (IBM SPSS 24).

Table 1
Spearman's ρ correlation coefficients of topographical, hydrological, sediment and vegetation parameters on the Biebrza Lower Basin floodplain. Bold coefficients indicate ρ ≥0.80. Grey coefficients indicate non-significant correlations. Analysis performed on all sampling points combined ($n = 18$).

	Elevation	Water depth	Deposition load	P-deposition	N-deposition	Dissolved N	Dissolved P	Aboveground biomass	Species richness
Distance from river (m)	**0.80****	-0.69**	-0.66**	-0.75**	-0.65**	-0.73**	-0.20	-0.59*	0.48
Elevation (m)		**-0.87****	-0.55*	-0.62*	-0.56*	**-0.82****	-0.01	**-0.87****	**0.83****
Water depth (m)			0.66**	0.70**	0.71**	0.73**	0.03	0.75**	-0.70*
Deposition load (kg ha^{-1})				**0.98****	**0.99****	0.61*	0.18	0.71**	-0.39
P-deposition (kg ha^{-1})					**0.96****	0.67**	0.14	0.73**	-0.45
N-deposition (kg ha^{-1})						0.58*	0.18	0.73**	-0.41
Dissolved N (mg l^{-1})							-0.18	0.41	-0.58
Dissolved P (mg l^{-1})								0.38	0.47
Abovegrond biomass (kg dry weight ha^{-1})									-0.43

** Correlation is significant at the 0.01 level (2-tailed).
* Correlation is significant at the 0.05 level (2-tailed).

4. Results

4.1. Correlations between topography, hydrology, sediment and vegetation

A Spearman's rho correlation analysis on all sampling points and all variables showed significant correlations ($p < 0.05$) among many (64%) of the variable combinations (Table 1).

Hydrological parameters (distance from the river, elevation and water depth in April) were all significantly correlated with each other. Sampling points at higher elevation above the river water level had lower water depths in April (ρ −0.87, $p < 0.01$).

Sediment and particulate nutrient deposition loads (total load, P load, N load) were all highly correlated (all ρ > 0.96, $p < 0.01$). Deposition loads of P and N were best related to, and increased with, water depth in April (all ρ > 0.66, $p < 0.01$) and distance from the river (all ρ > 0.65, $p < 0.05$), while lower correlations were found with elevation (all ρ > −0.55, $p < 0.05$). All correlations between sediment and particulate nutrient loads and hydrological parameters were significant.

Concentrations of dissolved N decreased significantly with elevation (ρ −0.82, $p < 0.01$) and distance from the river (ρ −0.73, $p < 0.01$) and were higher at locations with greater water depth in April (ρ 0.73, $p < 0.01$). No significant correlations with hydrological variables were found for dissolved P, or with aboveground biomass and species richness for both dissolved N and P.

4.2. Vegetation parameters

Related to hypothesis 3, aboveground biomass increased with inundation depth in April (ρ 0.75, $p < 0.01$). A decreasing trend with distance from the river was also observed (ρ −0.59, $p < 0.05$). Particulate nutrient loads correlated significantly with aboveground biomass (all ρ > 0.71, $p < 0.01$). Aboveground biomass (Fig. 3) was generally higher in Olszowa Droga (2.6–10.2 × 10^3 kg dry wt ha^{-1}) than in Kołodzieje (1.9–5.0 × 10^3 kg dry wt ha^{-1}) and Mscichy (2.7–4.6 × 10^3 kg dry wt ha^{-1}). Reeds had higher aboveground biomass (6.2 × 10^3 kg dry wt ha^{-1}, $p < 0.05$) than tall sedges (3.8 × 10^3 kg dry wt ha^{-1}) and small sedges (2.4 × 10^3 kg dry wt ha^{-1}), and compared with small sedges the sediment they trapped contained more N and P ($p < 0.05$).

Species richness (as a measure for biodiversity) was only significantly correlated with elevation (ρ 0.83, $p < 0.01$) and water depth in April (ρ −0.70, $p < 0.01$). In Olszowa Droga, relatively high species richness was observed at one elevated point on the sandy river bank and towards the edge of the floodplain, leading to absence of a linear lateral trend. In depressions and old river beds near the river channel in all three transects, extensive monocultures of highly productive *Phragmites australis* or *Glyceria maxima* were observed. Mean species richness was highest in small sedges (19.00) and lowest in reeds (7.25).

4.3. Spatial patterns in inundation, river water flooding and particulate nutrient deposition

At the peak of the flood (April), almost all sampling points, including the sampling points at the edge of the floodplain, were under water (to a depth of at least 5 cm), i.e. in all transects, the edge of inundation was between the floodplain edge and the sampling point furthest from the river (Mscichy: > 2000 m; Olszowa Droga: ~900 m; Kołodzieje: ~900 m, see Fig. 3). Analysis of the hydrochemistry of the inundation water at the height of the flood (April) showed river water to be present in (part of the) inundation water in all transects; however, the lateral extent of the influence of river water varied between the transects. Additional evidence of presence of river water was obtained from inundation water flow measurements. Flowing water during peak flow (Fig. 3) was assumed to indicate river water or mixing of river water and other water sources.

In Olszowa Droga, an increase in pH (7.4–7.8), NO_3^- (0.2–0.3 mg l^{-1}) and SO_4^{2-} (13–17 mg l^{-1}) was seen between sampling points OD1 and OD2 (for sampling locations, see Fig. 3), indicating mixing of river water with mineral-poor atmospheric water or groundwater. K^+ did not increase similarly. No flowing water was observed at OD1 (0.00 m s^{-1}), in contrast to at OD2 (0.02 m s^{-1}) and at OD4, OD5 and OD6. At OD3, water was also stagnant, possibly due to flow being impeded by the upstream river dune, and (resulting) extensive emergent vegetation. The extent of river water influence was interpreted as located between OD1 and OD2.

In Mscichy, NO_3^- concentrations increased between MS3 and MS4 (from 0.14 to 0.27 mg l^{-1}), while K^+ concentrations increased most between MS2 and MS3 (from 1.1 to 2.9 mg l^{-1}). SO_4^{2-} and pH revealed contrasting trends (SO_4^{2-} peaked in the central part whereas pH increased towards the floodplain edge). Flow velocities were low at all sampling points that could be reached. The extent of river water influence was interpreted as located between MS3 and MS4.

In Kołodzieje, K^+ increased between KOL1 and KOL2 (from 1.1 to 3.8 mg l^{-1}), while SO_4^{2-} and NO_3^- showed no clear trends. pH was highest at KOL1. In April, surface water was stagnant at KOL1 (too shallow to measure, visual observation), while water was flowing at KOL2 (0.006 m s^{-1}). The extent of river water influence was interpreted as located between KOL1 and KOL2.

Using the abovementioned hydrochemical characteristics and flow measurements, the lateral extent of the influence of river water chemistry was estimated for each transect (Mscichy: 850 m; Olszowa Droga:

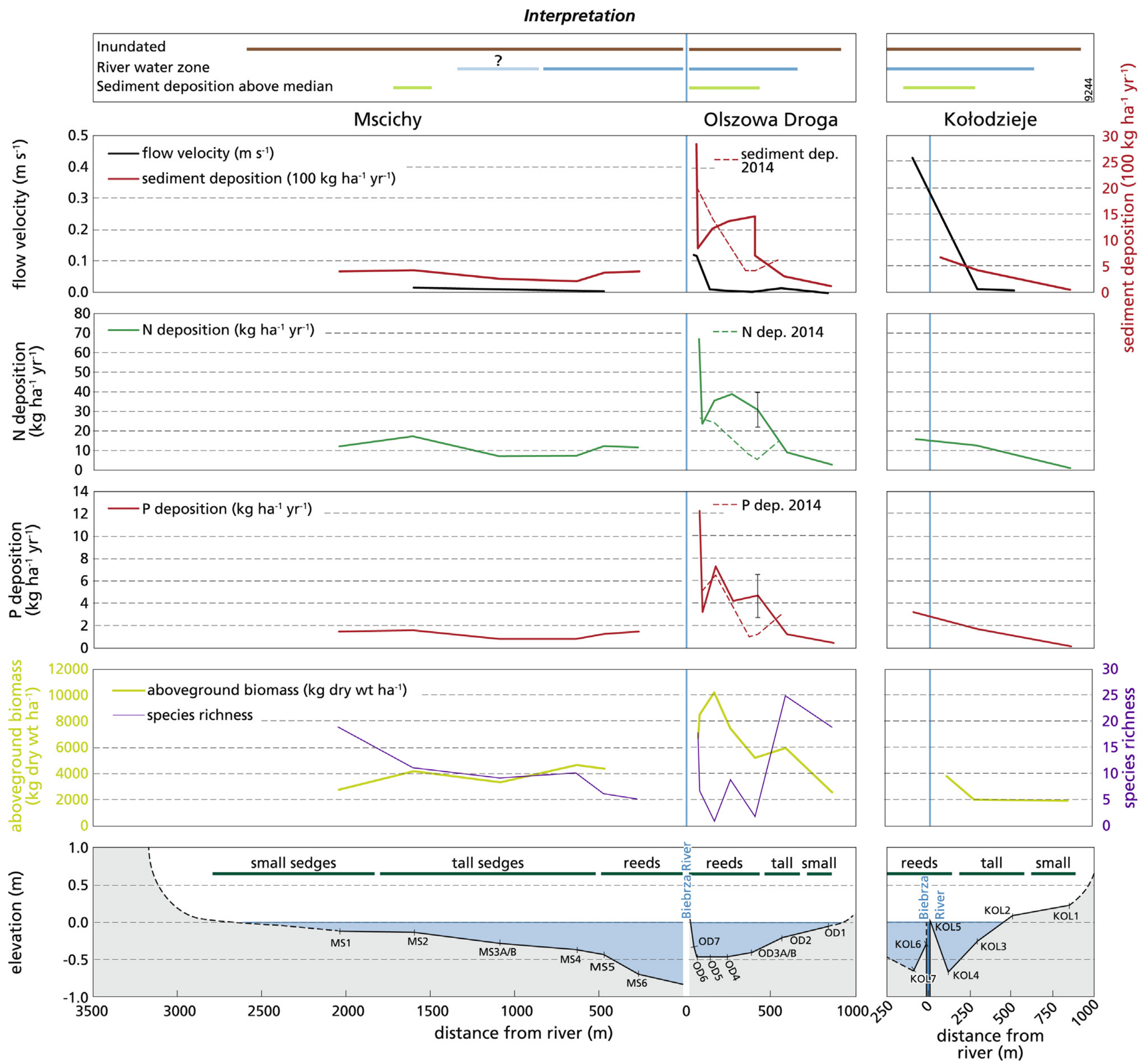

Fig. 3. Interpreted inundation zones, river water zones, and above-median sediment deposition zones along the transects (16 April 2015) and (top to bottom) inundation water flow velocities, sediment deposition, particulate nutrient deposition (N and P), aboveground biomass and species richness, and topography. Error bars indicate range of values for duplicate samples.

700 m; Kołodzieje: 700 m; see Fig. 3).

Sediment deposition loads ranged from 37 to 2875 kg ha^{-1} yr^{-1} (Fig. 3). Sedimentation patterns decreased gradually over the transects with distance from the river, but for the Mscichy transect were higher again at the floodplain edge, which was outside the zone that flooded with river water.

5. Discussion

5.1. The edge of inundation and of river water

The edge of inundation on the Biebrza floodplain is not the edge of river-derived nutrient input (H1): our findings related to dissolved water quality (Fig. 3) and inundation water velocity (Fig. 3) have enabled us to demonstrate that river water does not cover the entire inundated area. In some parts of the floodplain, inundation water also originates from rainwater, snowmelt and exfiltration of groundwater (Chormański et al., 2011; Keizer et al., 2014). We therefore cannot reject hypothesis 1.

However, one of the difficulties in our study was the determination of the exact location of the edge of the river water zone. In our study, the indicators of river water as used in Keizer et al. (2014) and Chormański et al. (2011), i.e. pH, NO_3^-, K^+ and SO_4^{2-}, revealed less clear patterns of higher values close to the river channel. A possible reason is that in the previous studies, between-year and local differences were averaged. In the Keizer et al. (2014) study, the indicators were based on averages of a large dataset spanning 12 years (2001–2012); in the study by Chormański et al. (2011), they were based on a large number (549) of water samples from one year, covering the entire floodplain.

Variations in the extent of river water inundation are related to interannual variations in peak discharge, ranging from 26.6 to 87.2 $m^3\,s^{-1}$ between 2001 and 2015, with median discharge of 70 $m^3\,s^{-1}$ between 1951 and 2009. Depending on yearly peak discharge, river water covers a narrow or broad stretch of the floodplain as observed for 2001–2012 according to Keizer et al. (2014). The discharge at sampling in April 2015 roughly equals the 2001 discharge (resp. 24 and 21 $m^3 s^{-1}$). In both years river water reaches only a relatively narrow part of the floodplain. In 2006 (45 $m^3 s^{-1}$), 2008 (54 $m^3 s^{-1}$) and 2009 (54 $m^3 s^{-1}$) higher discharges were observed, although still below-median discharge, but for Mscichy transect still no river water was observed at the sampling points of 2015 (see Fig. 3) (except one point in 2006) (Keizer et al., 2014). Therefore the patterns of river water inundation we deduced from the used indicators allowed us to infer general trends and approximate borders for the Kołodzieje and Olszowa Droga transects. For the Mscichy transect, however, lateral trends in SO_4^{2-} and pH did not follow the general pattern of decreasing with distance from the river. Higher pH (but also higher EC, Cl^- and Ca^{2+}) towards the edge of the floodplain indicated a possible influence of mineral-rich groundwater or pollution from nearby hamlets and agricultural activity on the bordering moraine plateau. For the Kołodzieje transect, pH was highest near the floodplain edge, and SO_4^{2-} was stable over the transect. No possible causes could be found for either of these patterns. The position of the edge of the river water zone in Olszowa Droga was further supported by sudden drops in EC and Cl^- (not presented) between OD2 and OD1. K^+ did not follow the general pattern, but no causes could be identified for this exception.

As an additional proxy for river-derived water we used inundation water flow measurements. These showed both flowing and stagnant water in the zone where hydrochemistry indicated flooding with river water, where stagnant water may possibly be related to blockage by extensive emergent vegetation or local topography. On the other hand, outside the river-flooded zone, inundation water flow velocities were all extremely low, never exceeding 0.015 $m s^{-1}$ and mostly recorded as 0.000 $m s^{-1}$, whereas average flow velocities in the river-flooded zone were 0.086 $m s^{-1}$ (standard deviation 0.15 $m s^{-1}$). The low flow velocities outside the river water zone may reflect slow throughflow of discharging groundwater.

5.2. The zone of high nutrient input

It appeared that, as was hypothesised (H2), neither the edge of inundation, nor the edge of river water inundation demarcated zones of high nutrient input. Instead, we found that particulate N and P deposition were better indicators for the zone of high nutrient input. Particulate nutrient deposition is highest close to the river and decreases with distance from the river (Fig. 3), because flow velocities decrease with distance from the river (Walling and He, 1998). Local depressions next to the river banks, in which water is deep, have high accumulation rates (*cf.* Walling and He, 1998). We therefore cannot reject hypothesis 2.

At the Mscichy transect, higher deposition rates were found both near the river and near the floodplain edge, despite low flow velocity (0.013 $m s^{-1}$) at the latter locations. Higher deposition rates near the edge might be related to resuspension of previously degraded peat, but there was not enough information to prove this. Also, throughflow of exfiltrated groundwater could cause slow-flowing inundation water here.

Because floods recede slowly in the Biebrza floodplains, only five out of 18 mats were above the inundation water level when collected at the end of May. Four of the remaining mats were under water less than 10 cm deep. For a further seven mats, water depth was between 10 and 15 cm. One mat was still under 20 cm water. The water depth of the remaining mat was not recorded. Local differences in water table drawdown inhibit exact estimation of the number of days the sampling location remained flooded after mat collection. Mats located close to the floodplain edge had been under shallow water and had little sedimentation; from our hydrochemical data we infer they were not covered with river-derived water. Mats closer to the river and under deeper water at collection had the highest particulate nutrient loads. If they had been collected after complete flood recession the particulate nutrient load would probably have been even higher, thereby further increasing the significant differences in particulate nutrient deposition with distance from the river. Early mat retrieval may also explain the relatively low particulate nutrient deposition at MS4 and MS5 (close to the river), which were both still inundated to a depth of 12 cm at the moment of mat collection.

Our findings suggest that deposition occurs mainly during the later stage of the flood, when inundation water flow slows and water on the floodplain becomes stagnant and hydrologically disconnected from the river. This assumption is supported by (unpublished) measurements from 2014 when a gradient with lower deposition rates was observed with increasing distance from the river. Despite capturing only deposition during a 6-week period during the final stage of the 2014 flood, deposition loads were in the same order of magnitude (5.8–26.3 $kg N ha^{-1} yr^{-1}$, 2.4–4.7 $kg P ha^{-1} yr^{-1}$, see Fig. 3) as the deposition measurements that included the start of the flood (current study (0.8–68.2 $kg N ha^{-1} yr^{-1}$ and 0.1–2.2 $kg P ha^{-1} yr^{-1}$) and a 2002 study (31.3 $kg N ha^{-1} yr^{-1}$, 6.5 $kg P ha^{-1} yr^{-1}$; Wassen and Olde Venterink, 2006)). Also, although upstream peak discharge differed considerably between the sampling years 2002 and 2015 (86 $m^3 s^{-1}$ and 27 $m^3 s^{-1}$ respectively), this did not affect deposition loads, which further supports the dominance of the falling limb of the flood event for particulate nutrient deposition. To test this explanation, further research should involve temporally explicit measurements of particulate nutrient deposition rates.

Secondly, our study revealed lower sedimentation rates than on other connected floodplains (Fig. 4). This can probably be attributed to the relatively low erosion and sediment transport capacity of the Biebrza river due to the low flow velocities at peak discharge both in the river and on the floodplain. The generally shallow slopes, limited soil disturbance and moist climate might have contributed to the low erosion, sediment transport and deposition observed. Whereas artificial fertiliser is still almost absent in the Biebrza catchment, increased use of artificial fertilisers (dissolved nutrients adsorb onto particles) and manure from intensive dairy and livestock farming (particularly in the Netherlands and Denmark) might explain high particulate nutrient concentrations in many other European and US rivers. Other floodplains in temperate regions mostly show N and P deposition a factor 2–4 higher (Fig. 4): floodplains in the Netherlands (reedlands: 210–240 $kg N ha^{-1} yr^{-1}$ (Olde Venterink et al., 2006)), US (multiple study sites), created wetlands (173–235 $kg N ha^{-1} yr^{-1}$ (Bernal et al., 2016), 164 $kg N ha^{-1} yr^{-1}$ (Anderson and Mitsch, 2006)); and a floodplain along a restored river channel in Denmark (114 $kg P ha^{-1} year^{-1}$ (Poulsen et al., 2014)).

Particulate nutrient deposition rates at the locations inundated by groundwater or precipitation water further from the river in the current study can be conceptually compared with the rates in hydrologically closed systems in other studies (Fig. 4). Wassen and Olde Venterink (2006) found particulate nutrient deposition rates of 0 $kg N ha^{-1} yr^{-1}$ and 0.22 $kg P ha^{-1} yr^{-1}$ for the part of the floodplain inundated with non-river-derived inundation water investigated in the current study. The nutrient deposition rates in locations where river water did not influence the surface water in our study (1.0–16.9 $kg N ha^{-1} yr^{-1}$; 0.4–1.7 $kg P ha^{-1} yr^{-1}$) were in the lower range of deposition compared to the rates found in closed depressional wetlands (14–53 $kg N ha^{-1} yr^{-1}$, 0.8–5.7 $kg P ha^{-1} yr^{-1}$; Craft and Casey, 2000; Johnston (1991) in Craft and Casey, 2000) and in hydrologically disconnected riparian wetlands (35–48 $kg N ha^{-1} yr^{-1}$; Noe and Hupp, 2005).

5.3. Productivity and biodiversity

Floodplain productivity and biodiversity correlate less with the extent of inundation than with hotspots of deposition of suspended river sediment (high particulate nutrient input), as was hypothesised (H3) (Fig. 3).

Aboveground biomass decreased concomitantly with deposition of

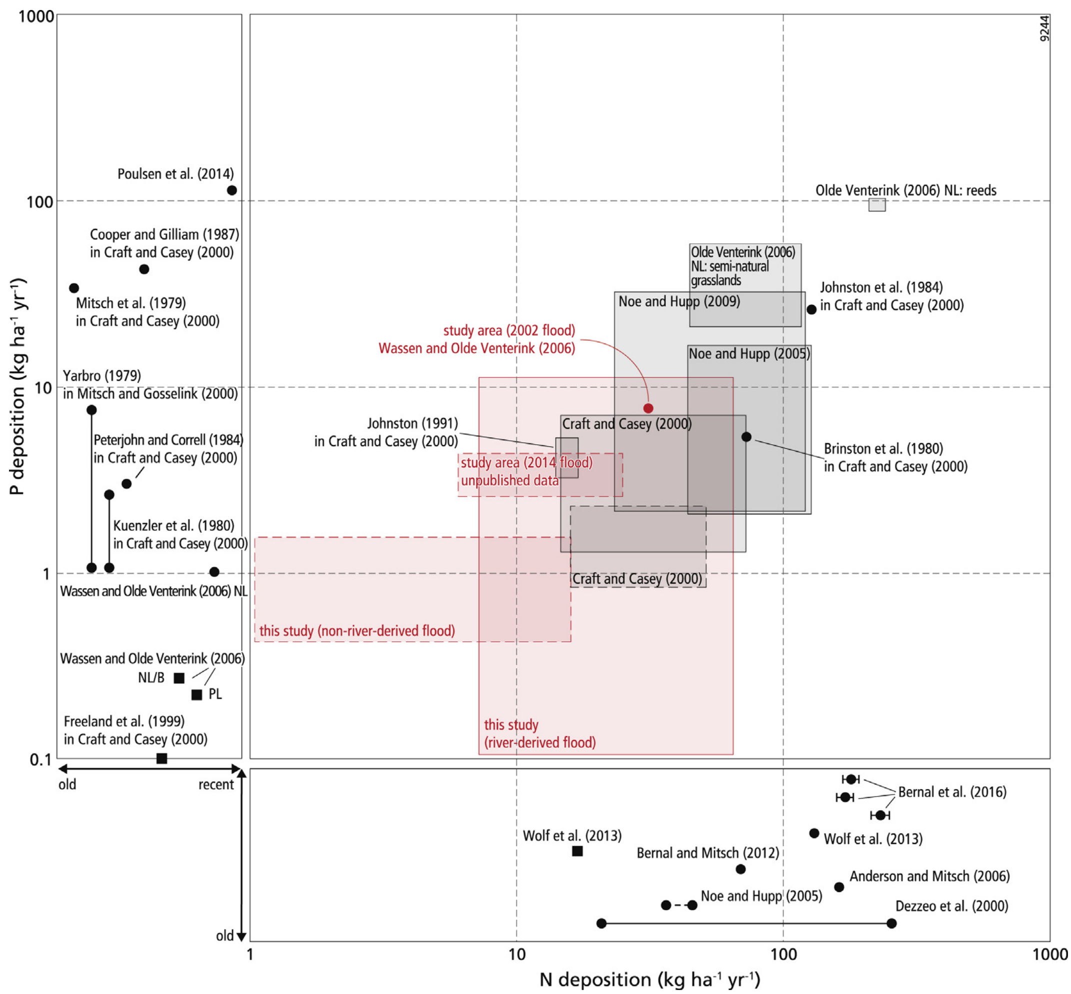

Fig. 4. Particulate N and P nutrient deposition ($kg\,ha^{-1}\,yr^{-1}$) of the Biebrza floodplain (red) compared to other freshwater wetlands: solid circles and solid-line boxes indicate systems open to river flooding; open squares, dashed boxes indicate systems disconnected from river flooding. The boxes and lines indicate ranges; points indicate averages. Error bars indicate standard deviation.

particulate nutrients, with distance from the river. The spatial gradients in particulate nutrient deposition and productivity are reflected in vegetation community patterns (Keizer et al., 2016), with high-productive freshwater marsh communities (*cf.* Pałczynski, 1986) occurring in the river-influenced zone (based on inundation water quality) of the studied floodplain. In areas with high particulate nutrient deposition rates, only highly productive communities of *Phragmitetum* and *Glycerietum maximae* were found and biodiversity was greatly reduced.

Lateral trends in biodiversity (measured as species richness) were not similar over the two transects with species richness data. Along the Mscichy transect, biodiversity increased with distance from the river. A similar trend was observed along the Olszowa Droga transect, except that here, biodiversity increased again on the sandy soil of the elevated river bank, yet productivity did not decrease. We conclude that hypothesis 3 is partly confirmed by our results. Only aboveground biomass was significantly correlated with deposition of particulate nutrients.

In riparian zones near the river channel, highly productive vegetation types are typically found (Chormański et al., 2011; Désilets and Houle, 2005). Olde Venterink et al. (2006) found similar patterns for Dutch floodplains, with high productivity only observed in reedbeds.

5.4. Implications of our findings

Our findings have important implications for the flood pulse concept. In our opinion, the flood pulse concept does not adequately describe hydrological processes that affect the flows of water, sediment and nutrients during flooding. Often other water sources besides river water are present, which implies that river-derived inundation water covers only part of the floodplain (e.g. Beumer et al., 2008; Keizer et al., 2014; Mertes et al., 1997; Rudorff et al., 2014). This suggests that river-derived dissolved nutrients do not reach all floodplain vegetation communities.

In river water most of the P and an important part of the N are transported in particulate form, attached to sediment, which reaches an even smaller area of the floodplain, across which deposition generally decreases exponentially during floods (Walling and He, 1998). Our findings show significantly lower deposition of N and P in areas not influenced by the river, which in terms of their deposition loads are similar to more hydrologically disconnected or depressional wetlands. We also found that most P was transported in particulate form, while dissolved P was very variable over the transect and not particularly enhanced in the river zone. Dissolved N, however, did show a higher concentration in river water, indicating significant transport of N in dissolved phase. Floodplain aboveground biomass decreased with distance from the river and showed significant correlation with deposition of particulate N and P, while no correlations were found with total dissolved nitrogen and P.

Potentially, these findings have important implications for floodplain ecosystem research and monitoring. Up till now, research has predominantly focussed on the role of dissolved nutrients in inundation floodwater for vegetation productivity. Consider for example the extensive monitoring of dissolved (not particulate) N and P for the EU Water Framework Directive. Although particulate nutrient input through sedimentation has been studied in several river floodplains (Fig. 4), its spatial patterns and relation to vegetation characteristics is an understudied topic (Hupp, 2000). This is particularly regrettable in view of the evidence of high particulate nutrient deposition in many floodplains (Craft and Casey, 2000; Kiedrzyńska et al., 2008; Noe and Hupp, 2005, 2009; Olde Venterink et al., 2006), and its link with vegetation productivity. Our re-evaluation of the flood pulse concept underlines the importance of including particulate nutrient measurements in floodplain ecosystem research. Deposited particulate nutrients are highly relevant, as they remain on the floodplain after flood recession and thus may become available to plants during the growing season. We therefore see a better understanding of the magnitude, fate and effects of particulate nutrient deposition on floodplain plant communities as a priority in floodplain ecosystem research.

One of the priorities for river science and management is the integration of concepts such as the flood pulse concept, with hydro (morpho)logy (Vaughan et al., 2009). Our study has shown that hydrological and sedimentological research can provide valuable insights that call for refinement of ecological river concepts. Such research improves understanding of the effects of flooding on floodplain ecosystem nutrient cycling, which is a prerequisite for adequate river–-floodplain management practices (Baldwin and Mitchell, 2000).

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